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HIGHEST ORDOVICIAN (HARTFELL SHALES) GRAPTOLITE FAUNAS FROM THE MOFFAT AREA, SOUTH SCOTLAND

BRITISH MUSEUM
NATURAL HISTORY

P. TOGHILL

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 19 No. 1
LONDON: 1970

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BY
PETER TOGHILL

Pp. 1–26; 16 *Plates*, 4 *Text-figures*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 19, *No.* 1 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.).

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 10 *April*, 1970

Price £3 5*s.*
(£3·25)

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By P. TOGHILL

CONTENTS

		Page
I.	Introduction	4
II.	Lithology and Graptolite Fauna of the highest Hartfell Shales, Main Cliff, Dobb's Linn	6
III.	Discussion of the highest Ordovician Graptolite Zones	7
IV.	The Caradoc-Ashgill boundary in the Graptolitic sequence	9
V.	Systematic descriptions	10
	Genus *Dicellograptus* Hopkinson	10
	Dicellograptus anceps (Nicholson)	10
	Dicellograptus complanatus Lapworth	12
	Dicellograptus ornatus Elles & Wood	14
	Dicellograptus ornatus minor subsp. nov.	16
	Dicellograptus moffatensis (Carruthers)	17
	Dicellograptus morrisi Hopkinson	17
	Dicellograptus carruthersi sp. nov.	18
	Dicellograptus cf. *elegans* (Carruthers)	19
	Genus *Pleurograptus* Nicholson	20
	Pleurograptus linearis (Carruthers)	20
	Genus *Leptograptus* Lapworth	20
	Leptograptus capillaris (Carruthers)	20
	Genus *Glyptograptus* Lapworth	21
	Glyptograptus nicholsoni sp. nov.	21
	Genus *Diplograptus* M'Coy	21
	Diplograptus fastigatus (Davies)	21
	Genus *Climacograptus* Hall	22
	Climacograptus hvalross Ross & Berry	22
	Climacograptus supernus Elles & Wood	22
	Climacograptus latus Elles & Wood	22
	Climacograptus styloideus Elles & Wood	22
	Climacograptus scalaris miserabilis Elles & Wood	23
	Genus *Orthograptus* Lapworth	23
	Orthograptus quadrimucronatus (Hall)	23
	Orthograptus truncatus truncatus (Lapworth)	23
	Orthograptus truncatus abbreviatus Elles & Wood	24
	Orthograptus truncatus pauperatus Elles & Wood	24
	Orthograptus truncatus socialis (Lapworth)	24
VI.	Acknowledgments	24
VII.	References	25

SYNOPSIS

The stratigraphy and graptolite fauna of the highest Ordovician (Hartfell Shales) graptolite zones of *Dicellograptus anceps*, *D. complanatus* and *Pleurograptus linearis*, exposed at Dobb's Linn, 10 miles north-east of Moffat, Scotland, is reviewed for the first time since Lapworth's original (1878) work. These three zones are 4·6 m. (15 ft.), 9·5 m. (31 ft.), and 4·9 m. (16 ft.) thick. The status and distribution of the zones is discussed, and it is suggested that the Ashgill Series is equivalent to only part of the *D. anceps* Zone. A large dicellograptid fauna is described including *D. carruthersi* sp. nov., and *D. ornatus* (=*D. complanatus* var. *ornatus* Elles & Wood) is considered a distinct species with a new subspecies *D. ornatus minor*. Lectotypes from original collections are chosen for *D. anceps*, *D. complanatus* and *D. ornatus*, and the remaining fauna includes *Glyptograptus nicholsoni* sp. nov., the first glyptograptid described from the higher Ordovician of Britain.

I. INTRODUCTION

The Hartfell Shales of the Moffat area (Lapworth 1876, 1878) incorporate the higher Ordovician graptolite zones of *Climacograptus wilsoni*, *Dicranograptus clingani*, *Pleurograptus linearis*, *Dicellograptus complanatus*, and *D. anceps*. These zones are generally accepted as standard divisions of the British Ordovician, and are accepted as being equivalent to part of the Caradoc Series, and the whole of the Ashgill Series. Exact correlations between shelly and graptolitic facies have always been controversial, particularly the exact placing of the Caradoc-Ashgill boundary in the graptolitic sequence. The controversies are in some measure due to the fact that the stratigraphy of the Hartfell Shales has not been reviewed since Lapworth's original work (1878), and the fauna not since Elles and Woods "Monograph" (1901–1918).

Although originally defined by Lapworth in 1876 the Hartfell Shales were not described in detail by him until 1878. They are the middle division of his condensed graptolitic sequence, the Moffat Series, overlain by the Birkhill Shales (Llandovery) and underlain by the Glenkiln Shales (lower Caradoc). The division was named after Hartfell Spa (4 miles north of Moffat) where according to Lapworth (1878 : 253) the beds were most perfectly exhibited. However because the beds there are highly contorted (Lapworth 1878 : 292) Lapworth used the section exposed on the Main Cliff (Pl. 1), Dobb's Linn, 10 miles N.E. of Moffat, as his standard sequence for the Hartfell Shales (Lapworth 1878 : 309, 315), except for the *wilsoni* Zone which was measured up at Hartfell Spa.

At Dobb's Linn the Hartfell Shales fall naturally into two lithological divisions, well exposed on the Main Cliff. A lower division of approximately 14 m. of black pyritic mudstones (zones of *Climacograptus wilsoni*, *Dicranograptus clingani*, and *Pleurograptus linearis*), and an upper division of equal thickness of barren grey mudstones with only a few thin graptolitic bands (*complanatus* and *anceps* Zones). These units were defined by Lapworth as the Lower and Upper Hartfell Shales, and the latter were sometimes referred to as the Barren Mudstones Group (Lapworth 1878 : 254), although the terms "zone of Barren Mudstone" and "Barren Mudstones" were usually used for the lower part of the Upper Hartfell Shales, later (1880a : 198) defined by him as the *complanatus* Zone.

The Hartfell-Birkhill boundary is in fact the Ordovician-Silurian boundary and the base of the Birkhill Shales (*persculptus* Zone) as exposed on the Main Cliff

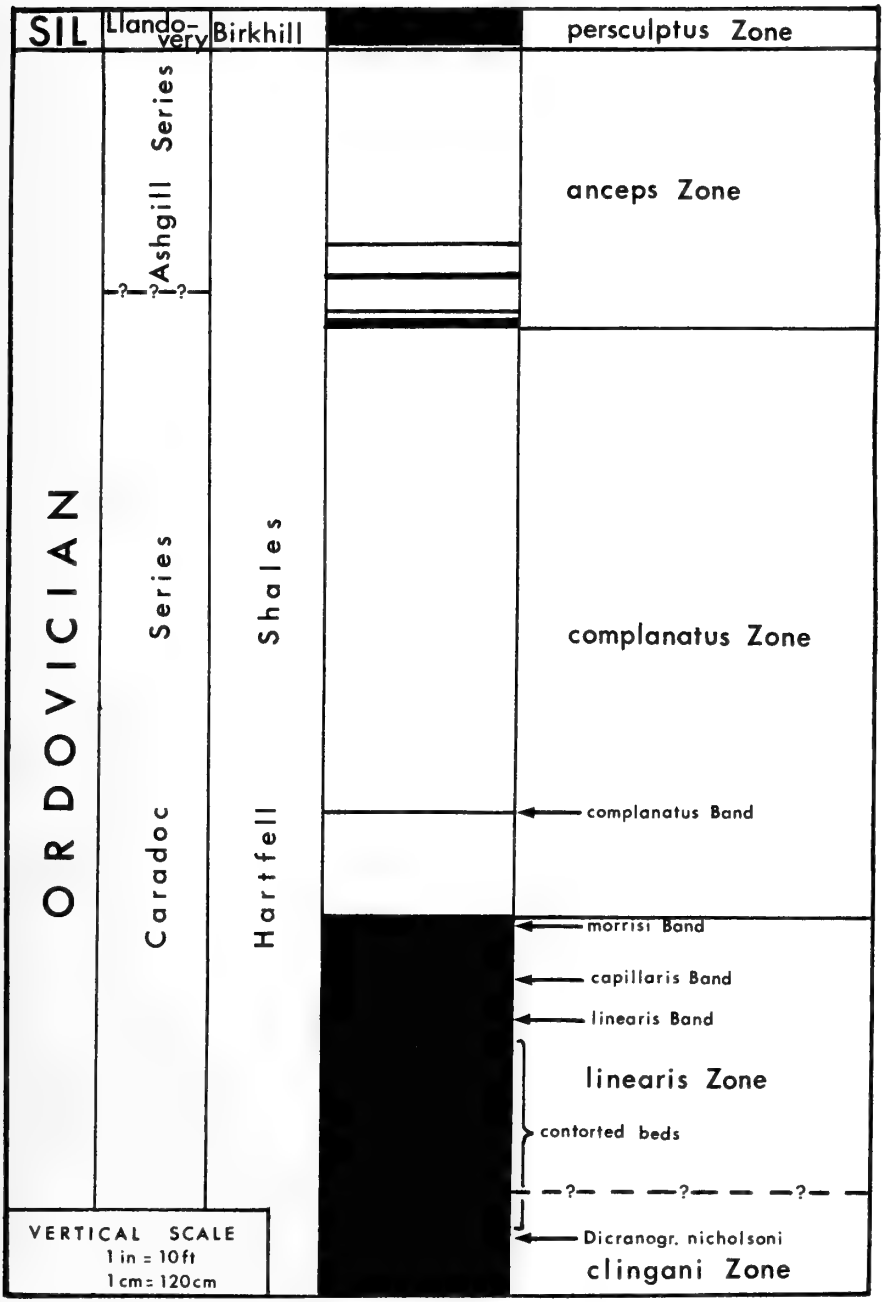

FIG. 1. Vertical section through the highest Ordovician of the Main Cliff, Dobb's Linn, showing the distribution of fossiliferous black mudstones, and (uncoloured) barren grey mudstones.

(Toghill 1968 : 658) has recently been set up as the standard base for the Llandovery Series and hence the Silurian System (Cocks, Toghill and Ziegler 1970 : in press).

This work covers the stratigraphy and graptolite fauna of the three highest Ordovician graptolite zones (*P. linearis*, *D. complanatus* and *D. anceps*) as exposed at the type locality of Dobb's Linn, and measured up on the Main Cliff, Dobb's Linn (Toghill 1968 : 656, Text-fig. 1).

II. LITHOLOGY AND GRAPTOLITE FAUNA OF THE HIGHEST HARTFELL SHALES, MAIN CLIFF, DOBB'S LINN

Zone of *Dicellograptus anceps*. 4·6 m. of beds exposed in the Main Cliff Section (Text-fig. 1) are assigned to this zone. The basal beds of the Birkhill Shales form a conspicuous overhang visible all along the Main Cliff (Pl. 1), and immediately overlie 3·1 m. of barren grey mudstones with thin soft pale coloured claystones (? pyroclastic). These barren mudstones overlie 1·4 m. of similar beds but with four rusty weathering black mudstones which are in descending order 51, 102, 25 and 152 mm. thick (Text-fig. 1). These four bands are highly fossiliferous containing the following common species: *Dicellograptus anceps* (Nicholson), *Climacograptus supernus* Elles and Wood, *C. scalaris miserabilis* Elles and Wood, and *Orthograptus truncatus abbreviatus* Elles and Wood. The following also occur, *Dicellograptus ornatus* Elles and Wood, *D. ornatus minor* subsp. nov., *D. complanatus complexus* Davies, *Climacograptus latus* Elles and Wood, *C. hvalross* Ross and Berry, *Diplograptus fastigatus* (Davies), *Nymphograptus velatus* Elles and Wood, ?*Neurograptus* sp., *Orthograptus truncatus truncatus* (Lapworth), *O. truncatus socialis* (Lapworth), *Glyptograptus nicholsoni* sp. nov. and *Plegmatograptus nebula* Elles & Wood.

Zone of *Dicellograptus complanatus*. The 152 mm. fossiliferous bed at the base of the *anceps* Zone overlies approximately 9·5 m. of grey and greyish green mudstones, massively bedded in the highest 4·6 m. but more shaley in the lower half. This unit is Lapworth's original "zone of Barren Mudstone" and immediately overlies black graptolitic mudstones of the *linearis* Zone.

About 1·5–1·8 m. above the base of this grey mudstone unit occurs a very conspicuous 40 mm. band of fossiliferous black shale, hereafter called the *complanatus* Band, well exposed at the northeast corner of the Main Cliff (Pl. 1), but covered by talus in the central part of the section. The thickness of barren grey mudstones between the band and the *linearis* Zone, given here as 1·5–1·8 m., is difficult to estimate owing to contortion of the beds. The *complanatus* Band is crowded with poorly preserved examples of *Dicellograptus complanatus* Lapworth, *Orthograptus truncatus socialis* (Lapworth), and *Climacograptus scalaris miserabilis* Elles and Wood, with rare examples of *Plegmatograptus nebula* Elles and Wood.

Zone of *Pleurograptus linearis*. The barren grey mudstones at the base of the *complanatus* Zone immediately overlie fossiliferous black pyritic mudstones with thin soft pale coloured (?pyroclastic) claystones. The highest 1·8 m. are fossiliferous throughout, but the zone is characterized by bedding planes crowded with one particular species almost to the exclusion of all others. This is particularly true of the orthograptids, but almost all species seem to have a gregarious habit.

The highest 0·3 m. of the zone contains one bedding plane crowded with *Dicello-*

graptus pumilus Lapworth, and *D. morrisi* Hopkinson, and another crowded with *Orthograptus truncatus pauperatus* Elles and Wood. The following also occur, *O. truncatus socialis*, *O. quadrimucronatus* (Hall), *Plegmatograptus nebula* Elles and Wood, *Dicellograptus* cf. *elegans* (Carruthers), *D.* cf. *elegans rigens* Elles and Wood, *D. moffatensis* (Carruthers), *D. carruthersi* sp. nov.

The underlying 0·6 m. of strata are not very fossiliferous but yield good specimens of *Orthograptus quadrimucronatus* together with *Climacograptus scalaris miserabilis*, *Dicellograptus pumilus*, and *D. carruthersi*.

The next 0·6 m. of strata contain one bedding plane crowded with *Leptograptus capillaris* (Carruthers), a species limited to this one horizon, and numerous other levels are crowded with *Orthograptus truncatus pauperatus*. *Climacograptus styloideus* Elles and Wood is restricted to this horizon which has yielded one example of *Pleurograptus linearis simplex* Elles and Wood, and also the following: *Leptograptus flaccidus* (Hall), *L. flaccidus arcuatus* Elles and Wood, *Dicellograptus moffatensis*, *D. morrisi*, *D. pumilus*, *D. forchammeri* (Geinitz). *Orthograptus truncatus truncatus*, *O. truncatus socialis*, *Climacograptus scalaris miserabilis* and *Plegmatograptus nebula*.

The underlying 0·6 m. of strata contains the only prolific horizon of *Pleurograptus linearis* (Carruthers), 1·5–2·1 m. below the top of the zone. The species occurs associated with *Leptograptus flaccidus*, *Orthograptus quadrimucronatus*, and *Orthograptus truncatus* s.l. (Lapworth).

Below this level on the Main Cliff there is a good deal of strike faulting, and the beds appear unfossiliferous until an horizon 3·4 m. below the *P. linearis* horizon yields *Dicranograptus nicholsoni* and *D. ramosus* indicating a level in the *D. clingani* Zone. On this evidence as much as 4·9 m. could be assigned to the *linearis* Zone.

III. DISCUSSION OF THE HIGHEST ORDOVICIAN GRAPTOLITE ZONES

The *Dicellograptus anceps* Zone has been accepted as the highest Ordovician graptolite zone in Britain, but apart from Scandinavia (Törnquist 1890) the zone fossil has not been recorded with any certainty from any other part of the world. The records from Australia (Thomas 1960) have not yet been figured. However, other elements of the fauna of the *anceps* Zone present in Scotland occur elsewhere in the world, in particular *Dicellograptus ornatus* which is widely recorded from N. America (Ruedemann 1947, Berry 1960, Churkin 1963), and Australia (Hall 1906). *Climacograptus hvalross* recorded here was originally found in the highest Ordovician of Nevada (Ross and Berry 1963). *Orthograptus truncatus abbreviatus* is widely recorded from North America and Australia, so there is little doubt that the *anceps* Zone has a world-wide distribution even if the index species has not. Because of the lack of this zone fossil in other areas the highest Ordovician is referred to as the zone of *Dicellograptus complanatus* or *D. complanatus ornatus* in Scandinavia, Australia, and North America (Tullberg 1882, Moberg 1911, Thomas 1960, Ross and Berry 1963).

In Britain *D. anceps* is abundant only in the Moffat area. However, Mrs. Gray recorded it (Peach & Horne 1899 : 525) from the Drummuck Group of the Girvan area, but strangely this is not cited by Elles and Wood (1904). Dr. Ingham has very kindly sent me graptolites which he has collected from the highest Ordovician

of the Girvan area, including a specimen of *D. anceps* from the Shalloch Formation (=Barren Flagstones) below the Drummuck Group (Text-fig. 4a) at Woodland Point. These beds immediately overlie the Upper Whitehouse Formation which contains *D. complanatus* in abundance. The significance of this in placing the Caradoc-Ashgill boundary in the graptolite sequence will be discussed below.

Contrary to popular belief, *D. anceps* was not recorded by Swanston and Lapworth (1877) from Northern Ireland, but was later found at Coal Pit Bay by Clark (1902), and at Pomeroy by Fearnsides, Elles and Smith (1907). Dr. Rushton of the Institute of Geological Sciences has kindly allowed me to see good specimens of *D. anceps* collected by the Geological Survey during a re-survey of the Northern Ireland One-Inch Sheet 36 (Belfast). Although recorded from Wales (Jones 1909, Pugh 1923), the preservation of these specimens is extremely poor.

The status of the *Dicellograptus complanatus* Zone has always been in doubt, not so much because of the validity of the species, which is in fact a well defined form with a wide distribution, but because the zone fossil is restricted to a 40 mm. band within a barren mudstone sequence at the type locality.

The *complanatus* Zone is defined here as all the barren mudstones occurring between the base of the lowest fossiliferous band of the *anceps* Zone, and the top of the black mudstones of the *linearis* Zone. The fauna is restricted to the *complanatus* Band 1·5–1·8 m. above the base of the zone. Lapworth (1878 : 316) stated that the fossiliferous band "near to the base of the zone of Barren Mudstone" contained *Dicellograptus forchammeri, Climacograptus scalaris*? and *Diplograptus truncatus*. He later (1880 : 160–161) described *D. complanatus* sp. nov. from this band, this new species presumably being what he had earlier (1878 : 316) referred to as *D. forchammeri*, and then (1880a : 198) he referred to the barren mudstones as the *D. complanatus* Zone. Lapworth stated (1880 : 161), in his original description, that *D. complanatus* occurred in the corresponding zone in the Hartfell Shales of County Down, and indeed Swanston (1877 : 111) recorded *D. forchammeri* from a black shale fragment in grey mudstones at Coal Pit Bay, but Dr. Rushton informs me that the Geological Survey have not found this locality during a re-survey of Coal Pit Bay. The *complanatus* Zone was accepted by Elles and Wood (1914) and has been accepted ever since, but with reservations.

Elles (1925 : 343) considered the fauna of the *complanatus* Zone to be "largely dwarfed" and the horizon to be "purely pathological", and stated that the fauna "seems to be almost invariably associated with a Barren Mudstone type of sediment. When the sedimentation is more normal a different fauna is found in which *Climacograptus styloideus* is the commonest and most characteristic graptolite". She concluded, "Whether this is a sub-zone of the *P. linearis* Zone or represents a still higher horizon cannot yet be stated definitely."

The more normal sedimentation to which Elles was referring was in the Berwyn Hills, where King (1923 : 492) obtained a fauna from the Pen-y-garnedd shales which Elles identified as including *Orthograptus quadrimucronatus, O. calcaratus basilicus, O. truncatus pauperatus*, and *Climacograptus styloideus*, and she there stated that this represented the highest *linearis* Zone! It is not at all clear why, in 1925, she thought this fauna to be equivalent to the *complanatus* Band as, except for

Orthograptus calcaratus, it is indeed typical of the *linearis* Zone as described here and the importance of *Climacograptus styloideus* in recognizing the zone has been emphasized by Bulman (1958 : 169).

I do not consider the *complanatus* Zone fauna to be dwarfed or pathological; indeed the zone fossil is more widely distributed than *Dicellograptus anceps*. The unfortunate fact about the zone is that it is based solely on a thin band in an otherwise barren sequence, and as the band is so near (1·5–1·8 m. above) to the *linearis* Zone it could be argued that it should be included in that zone (Elles 1937). However, Dr. Ingham has kindly loaned me material from the Upper Whitehouse Formation of the Girvan area, and this horizon contains abundant *D. complanatus*, as originally indicated by Lapworth (1882), some of which (Text-fig. 4b) are identical with those figured here from Dobb's Linn (Text-figs. 2g–l), and others have a smaller axial angle and appear intermediate between *D. complanatus* and *D. anceps*. There also occurs at this horizon *D. ornatus minor* subsp. nov., a form characteristic of the *anceps* Zone at Dobb's Linn. Thus at Girvan we have intermingling of the Dobb's Linn *anceps* and *complanatus* Zone faunas, and Girvan is providing faunas from a level equivalent to the Barren Mudstones at Dobb's Linn above the *complanatus* Band and below the *anceps* Zone, where it is possible that (if the beds were fossiliferous) the ranges of *D. anceps* and *D. complanatus* overlap. The probability that a more detailed graptolite sequence may yet come out of the Girvan sequence at this level is reason enough for provisional retention of the *complanatus* Zone.

The status of the *P. linearis* Zone is on much surer ground, but the present description of the fauna has provided some interesting results, most important of which concern the vertical restriction of *Leptograptus capillaris* and the zone fossil and the abundance of *Dicellograptus pumilus* and *D. morrisi* at the very top of the zone. No dicranograptids occur at all, the presence of these indicating the *D. clingani* Zone or lower. In the absence of the zone fossil *Leptograptus capillaris* and *Climacograptus styloideus* are very characteristic of the zone. In Dr. Ingham's collections from Girvan *P. linearis* occurs at the very top of the Lower Whitehouse Formation. In Northern Ireland it has been recorded by Clark (1902) and Pollock & Wilson (1961). Elsewhere in the world *P. linearis* is rare but has been recorded from Australia (Sherrard 1954, Thomas 1960), and a single specimen from North America (Ruedemann 1947).

IV. THE CARADOC–ASHGILL BOUNDARY IN THE GRAPTOLITIC SEQUENCE

The *P. linearis* Zone is generally accepted as being the highest division of the Caradoc Series in the graptolitic sequence, and the zones of *D. complanatus* and *D. anceps* are usually equated to the whole of the Ashgill Series (Whittard 1960).

Exact correlations between graptolitic and shelly facies of the upper Ordovician have always been controversial because of the lack of graptolites in the classic shelly Caradoc and Ashgill sequences of Wales, the Welsh Borders and the Lake District. However the Girvan area does provide a mixed shelly and graptolitic fauna at these horizons, and the following discussion is based entirely on material kindly loaned me by Dr. Ingham who is actively working on the upper Ordovician trilobites of the area.

As stated earlier, Mrs. Gray recorded *D. anceps* from the Drummuck Group of the Craighead Inlier (Peach and Horne 1899 : 525) and Dr. Ingham has now obtained two good specimens from the higher part of the Shalloch Formation (=Barren Flagstones) which underlies the Drummuck Group. Ingham also (1966 : 473) obtained *D. anceps* from the Middle Ashgill of Cautley and suggested (1966 : 488) that the lowest Ashgill at Cautley should, on the evidence of trilobite faunas, be equated with the Lower Drummuck Group of Girvan. Thus if the latter is basal Ashgill it overlies beds (the Shalloch Formation) which contain *D. anceps*, and thus the Ashgill Series is only represented by the upper part of the *anceps* Zone.

Dr. Ingham's preliminary studies of the trilobite faunas of the Upper Whitehouse and lower Shalloch Formations seem to confirm this, for they show Pusgillian (highest Caradoc) affinities, and yet contain *D. complanatus*, *D. anceps* and *D. ornatus minor* indicating the *complanatus* and *anceps* Zones. If the Pusgillian is accepted as the highest stage of the Caradoc Series it is thus equivalent not only to part of the *linearis* Zone (Dean 1959 : 149), but the whole of the *complanatus* Zone (as originally suggested by Bancroft in 1945), and extends up into the base of the *anceps* Zone. The Caradoc–Ashgill boundary thus lies at some level in the *D. anceps* Zone, and this is the highest level in the graptolitic sequence so far suggested for this boundary.

V. SYSTEMATIC DESCRIPTIONS

Suborder DIDYMOGRAPTINA Lapworth 1880 (emend. Bulman 1963)

Family ***DICRANOGRAPTIDAE*** Lapworth 1873

Genus ***DICELLOGRAPTUS*** Hopkinson 1871

Dicellograptus anceps (Nicholson)

(Pl. 2, Pl. 3, figs. 2–7; Text-figs. 2a–f, 4a)

1867 *Didymograpsus anceps* Nicholson: 110, pl. 7, figs. 18–20.
1870 *Didymograpsus anceps* Nicholson: 351, pl. 7, fig. 5.
1871 *Dicellograpsus anceps* (Nicholson); Hopkinson: 335, pl. 1, figs. 5a–b.
1876 *Dicellograptus anceps* (Nicholson); Lapworth: pl. 4, fig. 82.
1877 *Dicellograptus anceps* (Nicholson); Lapworth: pl. 7, fig. 5.
1890 *Dicellograptus anceps* (Nicholson); Törnquist: 21–23, pl. 2, figs. 16–19.
1904 *Dicellograptus anceps* (Nicholson); Elles and Wood; 141–143, pl. 20, figs. 3a–e.

Diagnosis. Stipes rigid, with relatively short and wide climacograptid thecae bearing mesial spines and having slight introversion, opening into deep excavations, numbering 10–8 in 10 mm. Stipes up to 1·5 mm. wide. Axial region sharply angled or rounded, axial angle 10°–30°, sometimes parallel sided. Sicula and virgella rarely preserved.

Lectotype. Q 3047, Nicholson Collection, Dobb's Linn, Moffat. ?Figured Nicholson 1867, pl. 7, fig. 19. Nicholson's graptolite collection was purchased by the B.M. (N.H.) in 1883 and it contains twelve specimens of *D. anceps*. Of these Q 3047 and Q 3065 could be the originals of his Pl. 7, figs. 19, 20, but it is impossible to be certain. Assuming the collection to be his original syntypes, a lectotype has been selected from them.

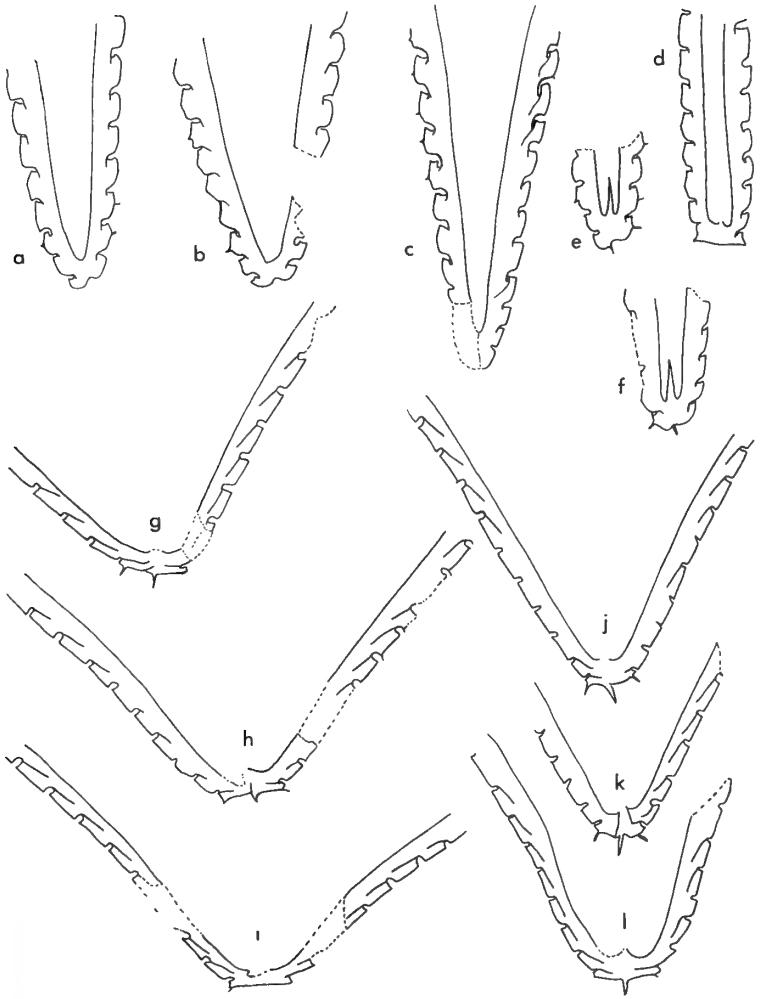

FIG. 2. a–f, *Dicellograptus anceps* (Nicholson), *anceps* Zone, Dobb's Linn, Moffat, Scotland, ×6. a, lectotype, Q3047, Nicholson Collection; b, paralectotype, Q3065; c, Q2753; d, Q2784; e, Q2857c; f, Q2857b. g–l, *Dicellograptus complanatus* Lapworth, *complanatus* Band, Dobb's Linn, Moffat, Scotland, ×6. g, lectotype, BU1072b, Lapworth Collection, fig'd Elles & Wood, 1904, pl. 20, fig. 1b; h, BU1072d; i, BU1072c, fig'd Elles & Wood, pl. 20, fig. 1d; j, Q2868a, Author's Collection; k, counterpart of Q2868a; l, Q2868b.

MATERIAL. The Nicholson Collection and twenty specimens collected by the author from the *anceps* Zone, Dobb's Linn, Moffat.

DESCRIPTION. The stipes are often long, up to 60 mm. and generally straight and rigid, but occasionally flexed either convex or concave. The axial region is typically sharply angled (Pl. 3, fig. 7), but is sometimes more rounded (Pl. 3, figs. 2, 5, 6),

and the axial angle is typically 20°–30°, but occasionally the stipes are parallel-sided (Pl. 3, figs. 2, 5). The stipes appear quite robust increasing in width from 0·5–0·8 mm. at the axial region to a maximum of 1·5 mm. The sicula is rarely preserved (hence the specific name), but when found (Pl. 2, figs. 6, 7; Text-figs. 2e, f) is 1·6 mm. long with a short virgella.

The thecae increase in length from 1·2 to 1·6 mm., number 10–8 in 10 mm., and overlap 1/3. They are of the climacograptid type with a conspicuous, but rounded, geniculum, and the free ventral wall shows continuous slight convex curvature, and the apertural region is slightly introverted opening into a deep excavation (Pl. 2, fig. 1). The apparent isolate apertures seen in Text-fig. 2c are due to a thin film of matrix. The thecae are relatively broad being about 5 times as long as wide. The proximal thecae bear a small spine midway along the free ventral wall, and the base of this is quite massive, and gives the thecae a double angled appearance (Text-fig. 2a).

Remarks. This is the youngest dicellograptid to occur in any abundance. The variations in the orientation of the stipes have not been noted before.

Associates and occurrence. The species occurs commonly in all the four fossiliferous horizons of the *anceps* Zone at Dobb's Linn (Text-fig. 1), associated with all the fauna of the zone. It occurs at Girvan in the Drummuck Group (Peach & Horne 1899 : 525), and Dr. Ingham has collected it from the underlying Shalloch Formation (=Barren Flagstones) (Text-fig. 4a). He also recorded the species from the Middle Ashgill of Cautley (Ingham 1966 : 473). Although recorded from Wales (Jones 1909; Pugh 1923) specimens are not well preserved. In Northern Ireland it was recorded from Coal Pit Bay by Clark (1902), and Pomeroy (Fearnsides, Elles and Smith 1907) and has recently been collected by the Geological Survey in the Belfast area.

The species occurs in the Upper *Dicellograptus* Shales of Sweden (Törnquist 1890) but Skoglund (1963 : 32) considered that the specimens identified by Törnquist (1890) as *D. anceps* were compressed specimens of *D. morrisi*. Although recorded from Australia (Hall 1898; Thomas 1960) it has not been figured, and there is only one very doubtful record from North America (Ruedemann 1947 : 376).

Dicellograptus complanatus Lapworth

(Pl. 4, 5, 6, fig. 1; Text-figs. 2g–l, 4b)

1880 *Dicellograptus complanatus* Lapworth; 160–161, pl. 5, figs. 17a–e.
1904 *Dicellograptus complanatus* Lapworth; Elles and Wood: 139–140, pl. 20, figs. 1a–d.
?1937 *Dicellograptus* cf. *complanatus* Lapworth; Sherrard and Keble: 309, fig. 8.
?1938 *Dicellograptus* cf. *complanatus* Lapworth; Harris and Thomas; pl. 3, fig. 103.
1947 *Dicellograptus complanatus* Lapworth; Ruedemann: 376, pl. 62, figs. 4–10.
1947 *Dicellograptus complanatus* var. *tenuis* Ruedemann: 378.
1960 *Dicellograptus complanatus* Lapworth; Berry: 73, pl. 20, fig. 1.
?1963 *Dicellograptus complanatus* Lapworth; Churkin: 63, fig. 39.
1963 *Dicellograptus complanatus* Lapworth; Skoglund: 33–36, text-fig. 10, pl. 1, fig. 3.

Diagnosis. Slender stipes with climacograptid thecae with little or no introver-

sion and straight supragenicular walls, numbering 8–12 in 10 mm. Stipes generally straight, up to 1 mm. wide and often up to 80 mm. long, axial angle 50°–90°. Sicula rarely preserved, virgella conspicuous but short, first two thecae bearing short mesial spines.

LECTOTYPE. BU1072b. The specimen figured, Elles and Wood, 1904, pl. 20, fig. 1b. Base of "Barren Mudstones", Dobb's Linn, Moffat, Lapworth Collection.

BU1072 is probably Lapworth's type slab and contains three specimens figured by Elles and Wood. However none of these, or any others on the slabs, can be matched exactly with Lapworth's original drawings, and so a lectotype has been selected from what may safely be considered his original syntypes.

MATERIAL. Lapworth's original collection (10 slabs), one figured specimen from the Wood Collection, and fifteen other specimens collected by the author. All from the *complanatus* Band, *complanatus* Zone, Main Cliff, Dobb's Linn, Moffat.

DESCRIPTION. The stipes are often very long, up to 80 mm., and generally straight, but occasionally flexed outwards at the proximal end (Pl. 4, fig. 4, Pl. 6, fig. 1).

The axial region is either rounded and open (Pl. 5, figs. 1, 3), or angled (Pl. 5, figs. 2, 4), and the axial angle is usually between 50°–90°, but increases to much more when double curvature occurs. Some of these variations in the axial region are probably due to distortion. The stipes are generally narrow increasing gradually in width from 0·4–0·6 mm. at the axial region to a maximum of 1 mm. The sicula is rarely preserved but is about 1·5 mm. long (Pl. 4, fig. 3), and a short but conspicuous virgella is always present. The first two thecae are relatively short (1 mm.) and grow horizontally, each bearing a short mesial spine. Later thecae are 1·5–1·6 mm. long and show a characteristic climacograptid appearance, with a very pronounced geniculum, which shows secondary thickening, giving the appearance of a small flange in profile view (Text-fig. 2h). The free ventral wall of each theca is generally parallel to the dorsal margin of the stipe, but in some cases there is slight introversion. The thecae overlap 1/3–1/2, number 10–8 in 10 mm., occasionally 12, but the latter figure is probably due to distortion.

REMARKS. This is a very distinct species, which may have developed from either *D. morrisi* (Hopkinson) or *D. forchammeri* (Geinitz), both of which it resembles somewhat, but is distinguished by its simple climacograptid thecae with no introversion. Specimens from Girvan sometimes appear intermediate between *D. complanatus* and *D. anceps*, and these forms occur at a level probably higher than the *complanatus* Band at Dobb's Linn. Ruedemann (1947 : 377) distinguished a var. *maximus* which had stipes 2·2 mm. wide with 6 thecae in 10 mm. No stipes wider than 1 mm. have been found at Dobb's Linn.

OCCURRENCE AND ASSOCIATES. At Dobb's Linn, *D. complanatus* is associated with crowds of *Orthograptus truncatus socialis* and *Climacograptus scalaris miserabilis* and is restricted to the *complanatus* Band. I have been unable to find the *complanatus* Band anywhere else in the Moffat area. Lapworth (1878 : 270) stated it occurred at Moory Syke but I have not been able to confirm this, and although the Barren Mudstones are well exposed at Craigmichan Scaurs and Belcraig Burn, they contain no fossiliferous horizons (Lapworth 1878 : 263, 284).

At Girvan *D. complanatus* occurs throughout the Upper Whitehouse Formation (Lapworth 1882) and in Dr. Ingham's collection is associated rarely with *D. ornatus minor* subsp. nov. in the highest beds of the formation. It has been recorded from Northern Ireland (Lapworth 1880 : 161; Fearnsides, Elles and Smith 1907) although not figured. Elsewhere in Europe, it occurs only in Sweden, in the Upper *Dicellograptus* Shales (Törnquist 1881, 1914, Tullberg 1882, Tornebohm and Henning 1904, Moberg 1911, Skoglund 1963). The latter author gave an account of the development of *D. complanatus* based on pyritized material.

D. complanatus occurs widely in North America (Ruedemann 1947, Berry 1960, Churkin 1963). It also occurs in Victoria and New South Wales, Australia (Thomas 1960), but the only figured specimens (Sherrard and Keble 1937; Harris and Thomas 1938) are referred to *D.* cf. *complanatus*.

Dicellograptus ornatus Elles & Wood

(Pl. 6, figs. 2–4; Text-figs. 3a, b)

1904 *Dicellograptus complanatus ornatus* Elles & Wood: 140–141, pl. 20, figs. 2a, b. non. fig. 2c.
1906 *Dicellograptus complanatus ornatus* Elles & Wood; Hall: 273, pl. 34, fig. 3.
1947 *Dicellograptus complanatus ornatus* Elles & Wood; Ruedemann: 377–378, pl. 62, figs. 16–20.
1960 *Dicellograptus complanatus ornatus* Elles & Wood; Berry: 74, pl. 20, fig. 3.
1963 *Dicellograptus complanatus ornatus* Elles & Wood; Churkin: pl. 3, fig. 40.
1963 *Dicellograptus complanatus ornatus* Elles & Wood; Ross and Berry: 103–104, pl. 6, figs. 8, 12, 13, 17, 19.

Diagnosis. Slender dicellograptid with introverted and ?introtorted thecae numbering 10–11 in 10 mm. Stipes straight up to 0·6 mm. wide and 60 mm. long, axial region square, axial angle 30°–40°. Sicula and virgella rarely preserved. First two thecae characterized by long and robust (?apertural) spines

Lectotype. SMA19332. Figured as *D. complanatus ornatus*, Elles & Wood, 1904, pl. 20, fig. 2b. *anceps* Zone, Dobb's Linn, Moffat.

Material. The lectotype and one other paralectotype.

Description. The stipes are long, up to 60 mm. and generally straight and narrow, widening gradually from 0·4 to 0·6 mm. The axial region is typically square and the axial angle 30°–40°. The sicula and virgella are not seen in either of the specimens. The first two thecae bear very conspicuous stout spines up to 4·2 mm. long, but it cannot be said with certainty whether these are apertural or mesial as they have coalesced with the whole of the theca, and it is impossible to pick out the aperture of the first two thecae. The remaining thecae are 1·2 to 1·5 mm. long and show marked introversion, narrowing, and possibly introtortion of the apertural region. The free ventral wall of each thecae is gently convex and a geniculum is well seen on the left hand distal thecae of the lectotype (Text-fig. 3a). The thecae overlap 1/3 and number 11–10 in 10 mm.

Remarks. The thecal form bears no resemblance to *D. complanatus* and so Elles and Wood's variety *ornatus* is considered as a distinct species. The thecal form is in

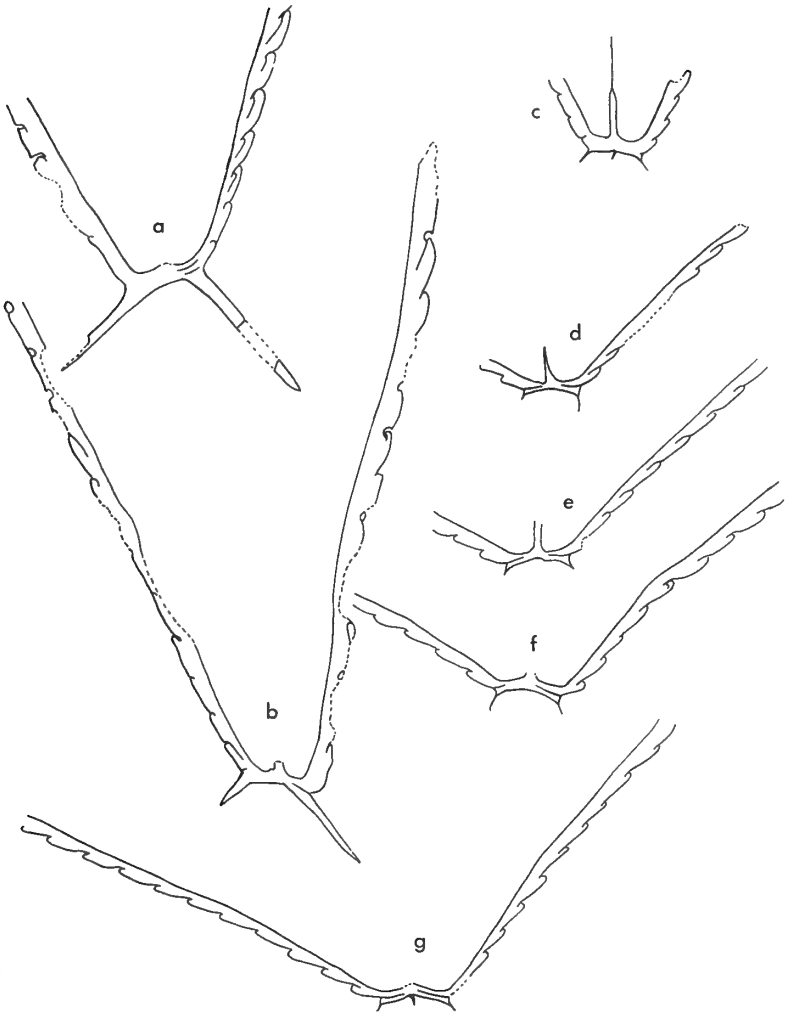

FIG. 3a–b, *Dicellograptus ornatus* Elles & Wood, *anceps* Zone, Dobb's Linn, Moffat, Scotland, ×6. a, lectotype, SM A19332, fig'd as *D. complanatus ornatus*, Elles & Wood, 1904, pl. 20, fig. 2b; b, paralectotype, SM A19331a, fig'd as *D. complanatus ornatus*, Elles & Wood, 1904, pl. 20, fig. 2a. c–g, *D. ornatus minor* subsp. nov., *anceps* Zone, Dobb's Linn, Moffat, ×6. c, Q3066, Nicholson Collection, ?fig'd as *Didymograptus flaccidus* (Hall), Nicholson, 1867, pl. 7, fig. 3; d, Q2766a; e, Q2766b; f, holotype, SM A19333, fig'd as *D. complanatus ornatus*, Elles & Wood, 1904, pl. 20, fig. 2c; g, Q2766c.

fact more like *D. forchammeri* (Geinitz). In describing specimens from North America both Ruedemann (1947) and Berry (1960) remarked on the exact similarity of their specimens with the descriptions of Elles and Wood, and yet I am suggesting that the latter's description was incorrect. I have examined specimens in collections

of the U.S. Geological Survey collected by Dr. Churkin from Alaska, and Idaho, and these specimens have much larger spines than the British forms, up to 8 mm. long. However the thecal form agrees with the description given above.

Occurrence and associates. *D. ornatus* is rare in the *anceps* Zone at Dobb's Linn and the only two specimens are associated with *Climacograptus supernus* and *Orthograptus truncatus abbreviatus*. In Britain it only occurs at Dobb's Linn, but even more spinose forms are characteristic of the highest Ordovician of North America. These horizons are there termed the *D. complanatus* or *D. complanatus ornatus* Zone (Ruedemann 1947, Churkin 1963, Jackson and Lenz 1962, Jackson, Steen and Sykes 1965, Ross and Berry, 1963). The species is also recorded from Australia (Hall 1906, Harris and Keble 1933, Thomas 1960).

Dicellograptus ornatus minor subsp. nov.

(Pl. 6, figs. 5–7; Text-figs. 3c–g)

?1867 *Didymograpsus flaccidus* (Hall); Nicholson: pl. 7, fig. 3.
1904 *Dicellograptus complanatus ornatus* Elles & Wood: pl. 20, fig. 2c.
?1947 *Dicellograptus complanatus arkansasensis* Ruedemann: 377, pl. 62, figs. 11–15.

Diagnosis. Very slender dicellograptid with introverted and ?introtorted thecae numbering 11–12 in 10 mm. Stipes straight up to 0·5 mm. wide, axial region square, axial angle 100°–120°. Sicula and virgella conspicuous. First two thecae bearing very short apertural spines.

Holotype. SMA19333, figured as *D. complanatus ornatus*, Elles & Wood, 1904, pl. 20, fig. 2c. *anceps* Zone, Dobb's Linn, Moffat.

Material. The holotype, five specimens collected by the author, and one specimen from the Nicholson Collection. All from the *anceps* Zone, Dobb's Linn.

Description. The stipes are generally short, straight, and very narrow, but one fragment (Pl. 3, fig. 1) 60 mm. long may be referable to this subspecies. The stipes widen from 0·2 mm. to a maximum of only 0·5 mm. The axial region is open and the first two thecae grow slightly downwards, rather than horizontal, so that the axial region has a slightly deflexed appearance (Text-figs. 3f, g). The axial angle is between 80°–120°. The sicula is well preserved on three of the specimens and is 1·5 mm. long with a conspicuous, but short virgella. One specimen bears a nema 1·5 mm. long. The first two thecae each bear a short apertural spine and are of a simple, almost leptograptid type. In most cases the spines are no more than small denticles on the ventral wall. The remaining thecae are 1·0–1·2 mm. long, overlap 1/3, number 11–12 in 10 mm., and have the same introversion of the apertural region as in *D. ornatus*.

Remarks. This subspecies has all the characters of *D. ornatus* but is less robust and lacks the proximal spines. In overall appearance it approaches species of *Leptograptus*, and also shows some resemblance to *Dicellograptus angulatus* Elles & Wood (1904: 150, figs. 3a–c), but this is supposedly a much earlier species. The specimen from the Nicholson Collection (Text-fig. 3c) occurs in association with *Dicellograptus anceps* and *Orthograptus truncatus abbreviatus*, and is quite probably that figured by

Nicholson (1867, pl. 7, fig. 3) as *Didymograpsus flaccidus*. *D. complanatus arkansasensis* (Ruedemann 1947 : 377, pl. 62, figs. 11–15), is said to be identical with *D. ornatus* but lacks the basal spines, so that it would on this evidence appear as *D. ornatus minor*. However, Ruedemann's figures show a much smaller axial angle and his variety is here only tentatively equated with *D. ornatus minor*.

Occurrence and associates. The subspecies is rare and restricted to the *anceps* Zone at Dobb's Linn, where it occurs with *D. anceps*, *Climacograptus supernus* and *Orthograptus truncatus abbreviatus*. Dr. Ingham has collected a specimen from the Upper Whitehouse Formation at Girvan, associated with *Dicellograptus complanatus*. I have recently examined two specimens from the Belfast area collected by the Geological Survey, and although referred to this subspecies, they are even more slender reaching a maximum width of only 0·25 mm.

Dicellograptus moffatensis (Carruthers)

(Pl. 8, Pl. 9, figs. 4, 5)

1858 *Didymograpsus Moffatensis* Carruthers: 469, fig. 3.
1904 *Dicellograptus moffatensis* (Carruthers): Elles & Wood: 157, pl. 23, figs. 1a–f.
1969 *Dicellograptus moffatensis* (Carruthers); Strachan: 189–190, text-fig. 2c, pl. 3, figs. 5, 6.

The type material of this species has recently been redescribed by Strachan (1969). The specimens here referred to the species *D. moffatensis* lack the membrane surrounding the axial region, but agree with Strachan's description in other features. It is the most robust of all the dicellograptids reaching a width of 1·5 mm.

At Dobb's Linn it occurs in the *linearis* Zone associated with *D. carruthersi* sp.nov., *D. morrisi*, and *Orthograptus truncatus*. This is the highest level from which it has been recorded as Elles & Wood (1904 : 159) recorded it only from the much lower zones of *N. gracilis* and *C. wilsoni*.

Records from even lower horizons are not genuine (Strachan 1969 : 190).

Dicellograptus morrisi Hopkinson

(Pl. 7, figs. 1–4; Text-figs. 4d–f)

1871 *Dicellograpsus Morrisi* Hopkinson: 24, pl. 1, figs. 2a–h.
1876 *Dicellograptus Morrisi* Hopkinson; Lapworth: pl. 4, fig. 85.
1904 *Dicellograptus Morrisi* Hopkinson; Elles & Wood: 155–157, pl. 21, figs. 6a–d.
1963 *Dicellograptus morrisi* Hopkinson; Skoglund: 31–32, pl. 1, figs. 1, 2.

Diagnosis. Dicellograptid with long rigid stipes widening throughout their length to 1·3 mm. Thecae numbering 12–10 in 10 mm. showing a rounded geniculum and marked introversion. Axial region rounded and open, axial angle 70°–80°. Sicula rarely preserved.

Material. Numerous specimens, all from the top of the *linearis* Zone, Dobb's Linn, Moffat.

DESCRIPTION. The stipes are often long, up to 50 mm. and generally straight and rigid, but occasionally show slight concave curvature (Pl. 7, fig. 1c). The axial region is usually rounded and open, and the axial angle typically 70°–80°. The stipes increase in width gradually but persistently from 0·4 mm. to a maximum of 1·2 mm. The sicula is rarely preserved but is about 1·3 mm. long (Text-fig. 4d) with a short virgella. The thecae increase in length from 1·2 to 1·5 mm., are relatively long and narrow, number 12–10 in 10 mm. and overlap 1/3. They show flowing sigmoid curvature of the ventral wall, with a rounded geniculum, and with a markedly introverted apertural region, opening into a deep excavation. The first two thecae bear short (?apertural) spines.

REMARKS. The persistent widening of the stipes is very characteristic of this species, and the thecal form is similar to *D. ornatus*. It is possible that *D. pumilus* Lapworth is in fact a young stage of *D. morrisi*. Skoglund (1963 : 32) stated that the proximal thecae (up to the 11th pair) bear stout mesial spines, but none of the specimens here described show this feature. He also stated that when obliquely compressed *D. morrisi* resembles *D. anceps* and suggested that specimens assigned to *D. anceps* by Törnquist (1890) were in fact distorted specimens of *D. morrisi*. I cannot see how any of the specimens here described as *D. morrisi* could appear as *D. anceps*.

OCCURRENCE AND ASSOCIATES. The species is abundant in the highest 0·3 m. of the *linearis* Zone at Dobb's Linn associated with *D. pumilus* (Pl. 7).

Dicellograptus carruthersi sp. nov.

(Pl. 7, figs. 5, 6; Text-fig. 4c)

DIAGNOSIS. Stipes rigid, up to 45 mm. long and 0·8 mm. wide. Thecae 12–10 in 10 mm. with marked introversion. Axial region sharply angled, axial angle 30°.

HOLOTYPE. Q 2915, *linearis* Zone, Dobb's Linn, Moffat.

MATERIAL. Numerous specimens all in the Author's Collection.

DESCRIPTION. The stipes are straight, rigid, and up to 45 mm. long, gradually increasing in width from 0·4 to 0·8 mm. The axial region is sharply angled and the axial angle typically 30°, but sometimes greater. The sicula is rarely preserved but has a short virgella, and the first two thecae bear mesial spines. The thecae are 1·2 mm. long, relatively narrow, overlap 1/2, number 12–10 in 10 mm. and show marked sigmoid curvature of the ventral wall, and introversion of the apertural region. They are of the same type as *D. morrisi*.

REMARKS. This new species is similar to *D. morrisi* but is narrower and has a much smaller axial angle.

OCCURRENCE AND ASSOCIATES. The species is common in the *linearis* Zone at Dobb's Linn, particularly in the highest 0·3 m., associated with *D. moffatensis*, *D. morrisi*, and *D. pumilus*.

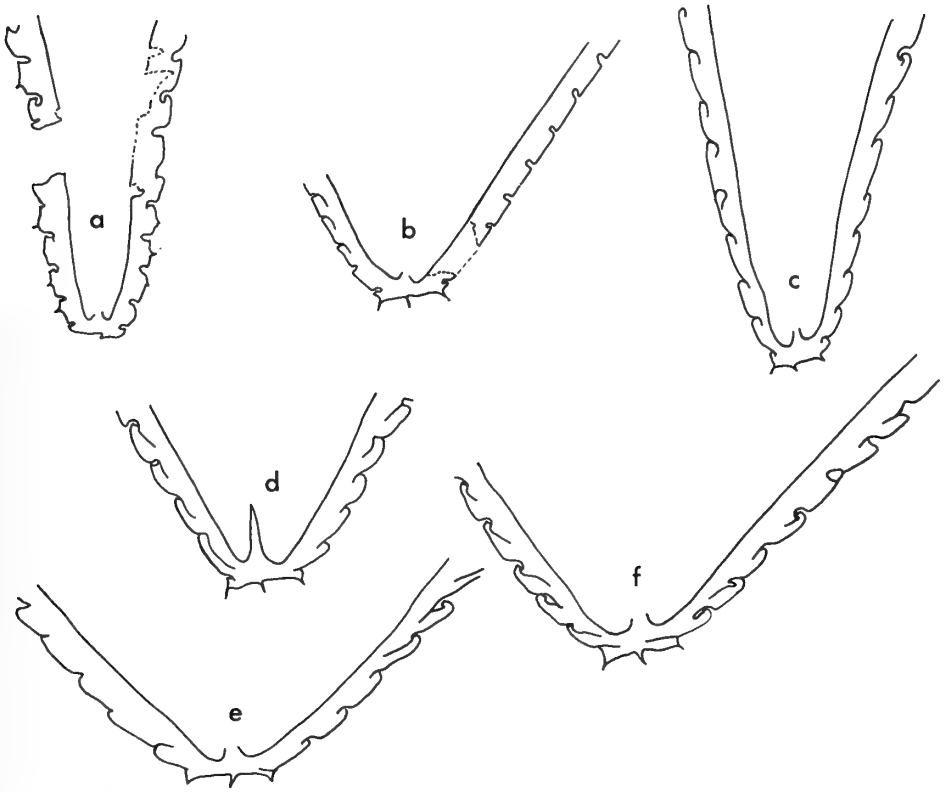

FIG. 4a, *Dicellograptus anceps* (Nicholson), HM.C802/1, Shalloch Formation (=Barren Flagstones), Woodland Point, Girvan, Ingham Collection, ×6. b, *Dicellograptus complanatus* Lapworth, HM.C785/1b, Upper Whitehouse Formation, Girvan, Ingham Collection, ×6. c, *Dicellograptus carruthersi* sp. nov., holotype, Q2915, ×6, *linearis* Zone, Dobb's Linn, Moffat. d–f, *Dicellograptus morrisi* Hopkinson, top of *linearis* Zone, Dobb's Linn, Moffat, ×7, d. Q2905a; e, Q2904b; f, Q2904a.

Dicellograptus cf. ***elegans*** (Carruthers)

(Plate 9, figs. 1–3)

1867 *Didymograpsus elegans* Carruthers: 369, pl. 2, fig. 16a.
1904 *Dicellograptus elegans* (Carruthers); Elles & Wood: 159, pl. 23, figs. 2a–e.
1969 *Dicellograptus elegans* (Carruthers); Strachan: 187–8, text-figs. 2a, b, pl. 3, fig. 1.

The type specimen of this species has recently been redescribed by Strachan (1969), and the most conspicuous feature of the species is the marked change in curvature of the stipes which (Strachan 1969 : 188) "curve first upwards, then outwards, then upwards again".

The specimens here referred to *D.* cf. *elegans* do not show the final upward curve

of the typical form, only showing one outward curve 3–4 mm. along the stipes. The thecae however have the characteristic marked introversion of the apertural region, but are closer together (12–10 in 10 mm.), as compared with 10–8 in 10 mm. in the typical form. The stipes reach 0·8 mm. in width which is rather less than the maximum of 1 mm. in the holotype.

These specimens are intermediate between *D. elegans* and *D. elegans rigens* Elles & Wood, a subspecies with rigid stipes. One specimen (Pl. 9, fig. 3) is referred to this latter form.

Occurrence and associates. *D.* cf. *elegans* and *D.* cf. *elegans rigens* occur rarely in the *linearis* Zone with *Orthograptus truncatus pauperatus*.

Family **LEPTOGRAPTIDAE** Lapworth 1880

Genus ***PLEUROGRAPTUS*** Nicholson 1867

Pleurograptus linearis (Carruthers)

(Pl. 10, figs. 1, 2, 4)

1858 *Cladograpsus linearis* Carruthers: 467, fig. 1.
1903 *Pleurograptus linearis* (Carruthers); Elles & Wood: pl. 16, fig. 7; pl. 17, figs. 1, 2.
1969 *Pleurograptus linearis* (Carruthers); Strachan: 186–7, text-fig. 1, pl. 2.

The type material of this species has recently been reviewed by Strachan (1969) and it is not intended to add to that description.

P. linearis has been found to be restricted to a level of 1·5–1·8 m. below the top of the *linearis* Zone where it occurs commonly, associated with *Leptograptus flaccidus*. A single specimen of *P. linearis simplex* has been found at a level 0·3 m. above the *P. linearis* horizon.

Genus ***LEPTOGRAPTUS*** Lapworth 1873

Leptograptus capillaris (Carruthers)

(Pl. 10, fig. 3)

1868 *Cladograpsus capillaris* Carruthers: 130, pl. 5, figs. 7, 7a.
1903 *Leptograptus capillaris* (Carruthers); Elles & Wood: 112, pl. 15, figs. 4a–d.
1969 *Leptograptus capillaris* (Carruthers); Strachan: 185–6, pl. 1.

The type specimen of this species has recently been reviewed by Strachan (1969). At Dobb's Linn it is restricted to a level 0·9 m. below the top of the *linearis* Zone where it occurs in abundance on one bedding plane with no associates.

Suborder DIPLOGRAPTINA Lapworth 1880 (emend Bulman 1963)

Family **DIPLOGRAPTIDAE** Lapworth 1873

Genus ***GLYPTOGRAPTUS*** Lapworth 1873

Glyptograptus nicholsoni sp. nov.

(Pl. 15, fig. 3)

DIAGNOSIS. Glyptograptid with short and markedly alternate thecae, which are closely set (16–13 in 10 mm.), and which show a marked distal decrease in overlap.

HOLOTYPE. Q2757. The only specimen, *anceps* Zone, Dobb's Linn.

DESCRIPTION. The only specimen found has a rounded, blunt, proximal end and increases gradually in width from 1·0 mm. to 1·4 mm. after 12 mm. The sicula is not visible. The thecae are relatively short, increasing in length from 0·8 mm. to 1·3 mm. and are closely set (16 in 10 mm.) at the proximal end but this value decreases distally to 13. They show flowing sigmoid curvature with a rather insignificant geniculum and are not far from being referable to *Orthograptus*. The thecae are markedly alternate, inclined at 25°, overlapping $\frac{1}{2}$ at the proximal end but the amount of overlap decreases sharply towards the distal end where they overlap only $\frac{1}{4}$, and here the thecae appear even more alternate.

REMARKS. This new species is the first glyptograptid to be described from the British higher Ordovician. It could be the ancestor of *G. persculptus* (Salter) or *G. avitus* Davies, but is closer to some of the Llandovery species described by Packham (1962).

It occurs in the *D. anceps* Zone associated with *D. anceps* and *Climacograptus supernus*.

Genus ***DIPLOGRAPTUS*** M'Coy 1850

Diplograptus fastigatus (Davies)

(Pl. 14)

1929 *Orthograptus fastigatus* Davies: 4, figs. 3–5.

DISCUSSION. Davies (1929 : 4) remarked on the differences between the proximal and distal thecae stating that the proximal thecae showed a pronounced curvature of the ventral wall, whereas the distal thecae were typical of *Orthograptus*.

The proximal thecae in fact show a climacograptid appearance (Pl. 14, fig. 5) and on this evidence the species is referred to *Diplograptus* s.s. It is abundant in, but restricted to, the *anceps* Zone.

Genus *CLIMACOGRAPTUS* Hall 1865

Climacograptus hvalross Ross & Berry

(Pl. 11, figs. 1–4, 7)

1963 *Climacograptus hvalross* Ross and Berry: 124, pl. 8, figs. 19, 26, 27.

Discussion. This is the first time that this species, first recorded from the highest Ordovician (*D. complanatus* Zone) of Nevada and Idaho, has been recorded elsewhere. The specimens here referred to it show all the characteristics described by the original authors including the membrane surrounding the initial parts of the conspicuous basal spines (Pl. 11, fig. 2). It is restricted to the *D. anceps* Zone associated with *D. anceps* and *Climacograptus supernus*.

Climacograptus supernus Elles & Wood

(Pl. 11, figs. 5, 6, 8–10)

1906 *Climacograptus supernus* Elles & Wood: 196–197, pl. 26, figs. 11 a–d.

Discussion. This species is restricted to the *D. anceps* Zone where it occurs quite commonly, associated with *C. latus* and *C. hvalross*. The slender basal spines are very characteristic as well as the slight temporary decrease in width after the first thecal pair.

Climacograptus latus Elles & Wood

(Pl. 15, figs. 1, 2)

1906 *Climacograptus latus* Elles & Wood: 204–205, pl. 27, figs. 3a–h.

Discussion. This rare species in the *D. anceps* Zone has only been recognized on distal fragments. These have a maximum width of 2·2 mm. and the thecae number 14–12 in 10 mm. Pl. 15, fig. 2 shows the characteristic rapid widening of the proximal portion although the extreme proximal end is missing.

Climacograptus styloideus Elles & Wood

(Pl. 13, figs. 1–4, 6)

1878 *Climacograptus styloideus* Lapworth: 312 (nomen nudum).
1906 *Climacograptus styloideus* Lapworth MS; Elles & Wood: 205–206, pl. 27, figs. 9a–e.
1963 *Climacograptus styloideus* Elles & Wood; Skoglund: 38–40, pl. 2, figs. 1–4, pl. 3, fig. 3.

Discussion. This species occurs quite commonly in, but is restricted to, the *P. linearis* Zone, where it is very characteristic and associated with *Dicellograptus morrisi* and *D. carruthersi*.

According to Lapworth (1878 : 312) a band with *C. styloideus* characterized the upper part of the *Dicranograptus clingani* Zone, but I have been unable to find this

species lower than the *linearis* Zone. Elsewhere in the world *C. styloideus* is considered a good indicator of the *linearis* Zone in the absence of the zone fossil (Bulman 1958 : 169).

Climacograptus scalaris miserabilis Elles & Wood

(Pl. 12)

non 1895 *Diplograptus* (*Glyptograptus*) *euglyphus* var. *angustus* Perner: 27, Pl. 8, figs. 14a, b.
1906 *Climacograptus scalaris* var. *miserabilis* Elles & Wood: 186–187, pl. 26, figs. 3a–h.
1963 *Climacograptus angustus* (Perner); Skoglund: 40–42, pl. 3, figs. 1, 2, pl. 4, fig. 7, pl. 5, fig. 6.

Discussion. Skoglund (1963 : 40) considered *C. scalaris miserabilis* Elles & Wood to be a junior homonym of *C. angustus* (Perner 1895). I do not agree with this, but I am sure that *C. angustus* (Perner) Skoglund 1963 is identical with *C. scalaris miserabilis* Elles & Wood though not the same as *C. angustus* (Perner 1895). The material on which Elles & Wood based their definition came from the *complanatus* Band at Dobb's Linn where it occurs in abundance. The very thin periderm and "ghost-like" appearance of the specimens from this horizon is very characteristic. It also occurs rarely in the *linearis* and *anceps* Zones, and ranges up into the basal Silurian.

Genus ***ORTHOGRAPTUS*** Lapworth 1873

Orthograptus quadrimucronatus (Hall)

(Pl. 13, figs. 10, 11)

1865 *Graptolithus quadrimucronatus* Hall: 144, pl. 13, figs. 1–10.
1907 *Diplograptus* [*Orthograptus*] *quadrimucronatus* (Hall); Elles & Wood 223–224, pl. 28, figs. 1a–d.

Discussion. This species occurs in the *linearis* Zone at Dobb's Linn, and although it does not range higher, I have not examined any lower horizons in detail. It is associated with *Orthograptus truncatus* s.l. (Lapworth).

Orthograptus truncatus truncatus (Lapworth)

(Pl. 16, figs. 3, 6)

1877 *Diplograptus truncatus* Lapworth: 133, pl. 6, figs. 1–7.
1907 *Diplograptus* [*Orthograptus*] *truncatus* Lapworth; Elles & Wood: 233–235, pl. 29, figs. 3a–e.

Discussion. This species is more characteristic of the *D. clingani* Zone, but Elles & Wood (1907 : 235) said it was also abundant in the *linearis* Zone. I have only found a few specimens in this zone, together with one wide (4·2 mm.) fragment from the *anceps* Zone (Pl. 16, fig. 6).

Orthograptus truncatus abbreviatus Elles & Wood

(Pl. 15, figs. 4–6, Pl. 16, figs. 4, 5)

1907 *Diplograptus* [*Orthograptus*] *truncatus* var. *abbreviatus* Elles & Wood: 235–236, pl. 29, figs. 6a–e.

Discussion. This subspecies is abundant in, but restricted to, the *anceps* Zone where it swarms on some bedding planes. The sub-fusiform appearance (Pl. 16, fig. 4) is very characteristic. It occurs with all the fauna of the *anceps* Zone but particularly with *Diplograptus fastigatus* (Davies), which species it originally included.

Orthograptus truncatus pauperatus Elles & Wood

(Pl. 16, figs. 1, 2)

1907 *Diplograptus* [*Orthograptus*] *truncatus* var. *pauperatus* Elles & Wood: 237, pl. 29, figs. 5a–d.

Discussion. This subspecies occurs in crowds on bedding planes in the *linearis* Zone, often to the exclusion of other forms (Pl. 16, fig. 1). It does not range higher.

Orthograptus truncatus socialis (Lapworth)

(Pl. 13, figs. 7–9, Pl. 16, fig. 7)

1880 *Diplograptus socialis* Lapworth: 166, pl. 4, figs. 13a–e.
1907 *Diplograptus* [*Orthograptus*] *truncatus* var. *socialis*: figs. 7a–e. Lapworth; Elles & Wood: 237–238, pl. 29, figs. 7a–e.

Discussion. This subspecies occurs in crowds in the *complanatus* Band at Dobb's Linn, and many of the specimens show good growth line structures. It occurs rarely in the *D. anceps* Zone.

VI. ACKNOWLEDGEMENTS

I would like to thank the many people who have allowed me to borrow specimens in their care, particularly; Dr. I. Strachan, Birmingham University; Dr. R. B. Rickards, Sedgwick Museum, Cambridge; Dr. A. W. A. Rushton, Institute of Geological Sciences. Dr. Ingham of the Hunterian Museum has very kindly sent me graptolites collected by him from Girvan, and allowed me to publish information on these.

I am also indebted to Dr. Strachan and Professor Bulman for reading and commenting upon the manuscript.

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DESCRIPTION OF PLATES

The photographs were taken by Mr. P. J. Green, except Plate 1 which was taken by the author. Specimens are in the British Museum (Natural History) (Q), Birmingham University (BU), Sedgwick Museum, Cambridge (SMA), and the Hunterian Museum. Glasgow (HM).

PLATE 1

The Main Cliff, Dobb's Linn, viewed from the north-east. The beds dip gently into the hillside and strike across the photograph. The total thickness of Ordovician Rocks exposed from the base of the section up to the base of the Silurian (Birkhill Shales) is approximately 30 m. (100 ft.). The lowest 9 m. (30 ft.) of the Birkhill Shales are massively bedded and form a conspicuous overhang.

Horizons indicated: 1, *D. anceps* Zone; 2, *D. complanatus* Zone; 2a, *D. complanatus* Band; 3, *P. linearis* Zone; 4, *D. clingani* Zone; 5, *C. wilsoni* Zone.

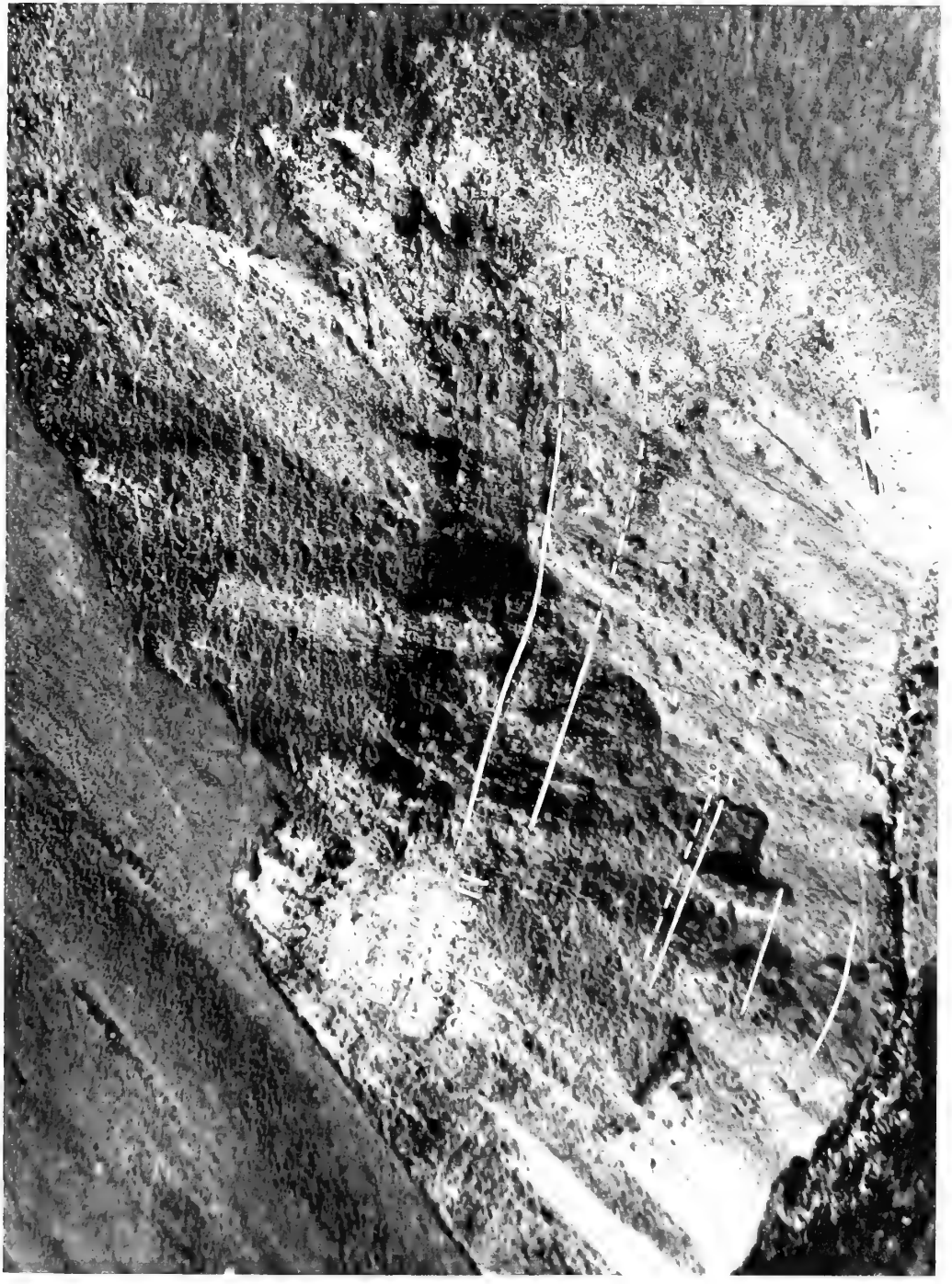

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PLATE 2

Dicellograptus anceps (Nicholson)

Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.

Author's Collection.

FIG. 1. Q 2753. ×8.

FIG. 2. Q 2792. ×5. Parallel sided form.

FIG. 3. Q 2844. ×4.

FIG. 4. Q 2857a. ×10. Associated with *Climacograptus scalaris miserabilis*.

FIG. 5. Q 2827. ×4. Distal stipes up to 1·5 mm. wide, associated with *Climacograptus scalaris miserabilis* and *Plegmatograptus nebula*.

FIG. 6. Q 2857c. ×10. Showing sicula.

FIG. 7. Q 2857b. ×10. Showing sicula.

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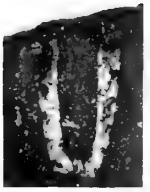

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PLATE 3

Dicellograptus sp.
Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

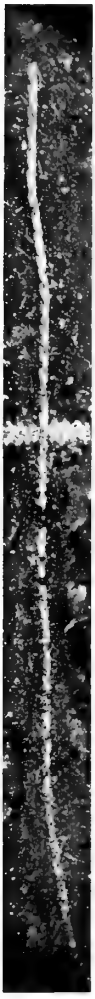
FIG. 1. Q 2856. ×2. Long fragment probably referable to *D. ornatus* sensu lato.

Dicellograptus anceps (Nicholson)
Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.
except Figs. 6, 7 which are Nicholson Collection.

FIG. 2. Q 2784. ×5. Parallel sided form.
FIG. 3. Q 2835. ×5.
FIG. 4. Q 2819a. ×4.
FIG. 5. Q 2791. ×5.
FIG. 6. Q 3065. ×2. Paralectotype. ? figured Nicholson 1867, pl. 7, fig. 20.
FIG. 7. Q 3047. ×2. Lectotype. ? figured Nicholson 1867, pl. 7, fig. 19.

Dicellograptus complanatus complexus Davies
Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 8. Q 2830c. ×4.



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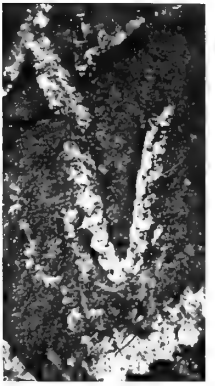

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PLATE 4

Dicellograptus complanatus Lapworth

Hartfell Shales, *complanatus* Band, *complanatus* Zone, Dobb's Linn, Moffat, Scotland.

Figs. 1, 5, Lapworth Collection, figs. 2–4, Author's Collection.

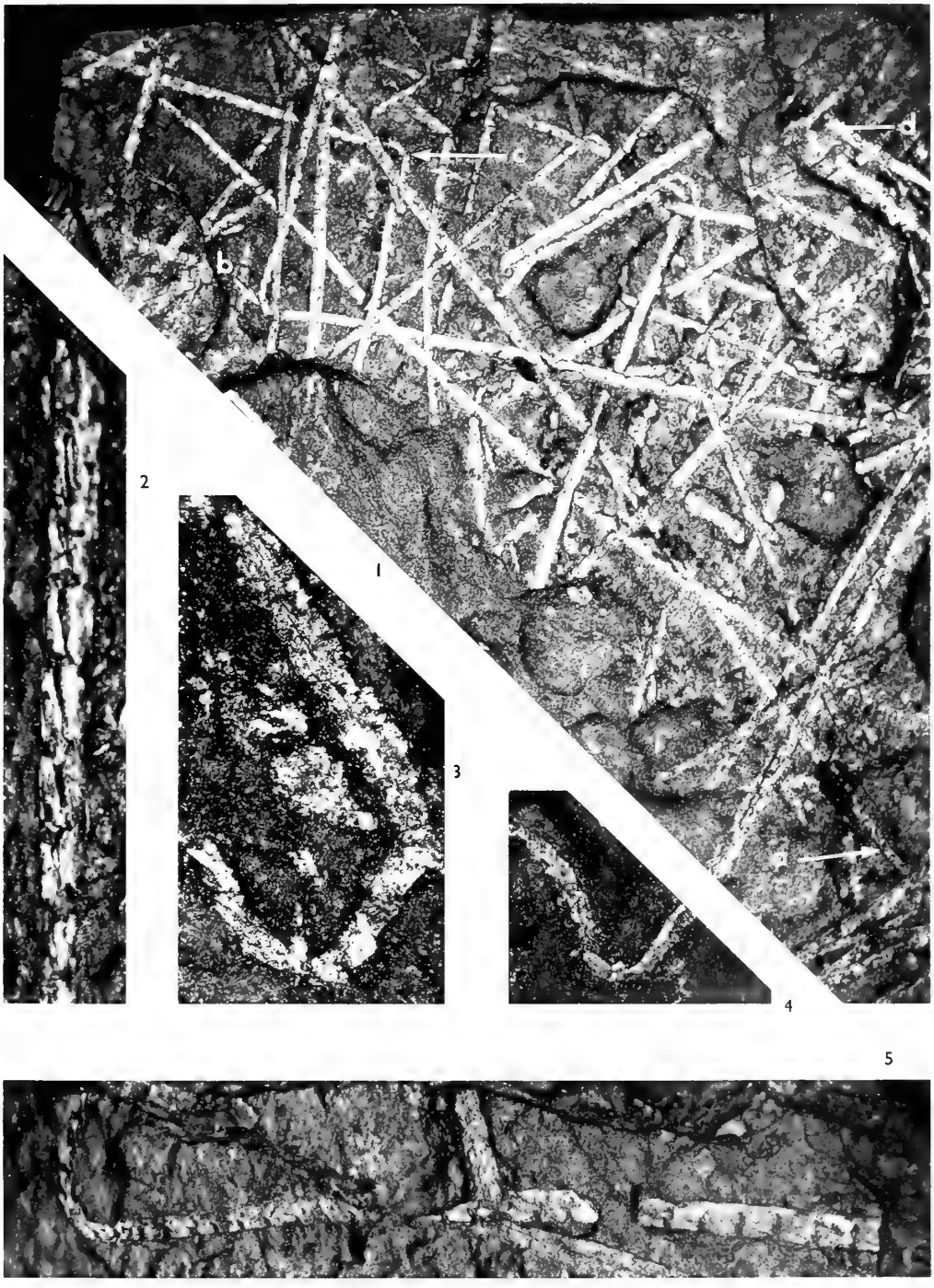
FIG. 1. BU1072. Lapworth's type slab. ×2. a. Paralectotype, figured, Elles & Wood, 1904, pl. 20, fig. 1a. b. Lectotype, figured, Elles & Wood, 1904, pl. 20, fig. 1b. c. Paralectotype, figured, Elles & Wood, 1904, pl. 20, fig. 1d.

FIG. 2. Q 2887. ×10. Distal thecae.

FIG. 3. Q 2871. ×10. Specimen with sicula, associated with *Climacograptus scalaris miserabilis*

FIG. 4. Q 2900. ×5. Specimen with curved stipes.

FIG. 5. BU1076. ×5. Figured, Elles & Wood, 1904: 139, fig. 84a.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b
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PLATE 5

Dicellograptus complanatus Lapworth

Hartfell Shales, *complanatus* Band, *complanatus* Zone, Dobb's Linn, Moffat.
Author's Collection.

FIG. 1. Q 2868b. × 10. Enlargement of specimen on FIG. 5.
FIG. 2. Q 2868a. × 10. Enlargement of specimen on FIG. 5.
FIG. 3. Q 2868d. × 10. Enlargement of specimen on FIG. 5.
FIG. 4. Q 2868c. × 10. Enlargement of specimen on FIG. 5.
FIG. 5. Q 2868. × 2.

1

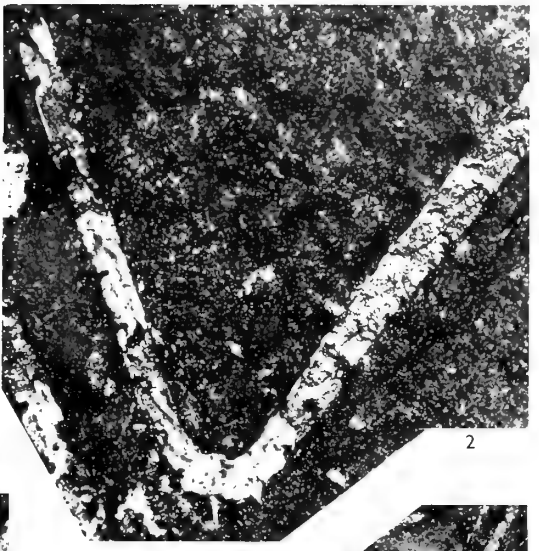

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PLATE 6

Dicellograptus complanatus Lapworth

Hartfell Shales, *complanatus* Band, *complanatus* Zone, Dobb's Linn, Moffat.
Lapworth Collection.

FIG. 1. BU1386. ×10. Specimen showing double curvature. Figured, Elles & Wood, 1904 : 139, fig. 84c.

Dicellograptus ornatus Elles & Wood

Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Elles Collection (Fig. 2) and Swanston Collection (Figs. 3, 4).

FIG. 2. SMA 19332. ×5. Lectotype, figured as *D. complanatus ornatus*, Elles & Wood, 1904, pl. 20, fig. 2b.

FIG. 3. SMA 19331a. ×5. Paralectotype, figured as *D. complanatus ornatus*, Elles & Wood, 1904 : 140, fig. 85a, pl. 20, fig. 2a.

FIG. 4. SMA 19331b. ×5. Counterpart of 19331a.

Dicellograptus ornatus minor subsp. nov.

Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Elles Collection (Fig. 5) and Author's Collection.

FIG. 5. SMA 19333. ×5. Holotype, figured as *D. complanatus ornatus*, Elles & Wood, 1904, pl. 20, fig. 2c.

FIG. 6. Q 2766a. ×10. Associated with *D. anceps*.

FIG. 7. Q 2766b. ×10. Specimen with well preserved sicula.

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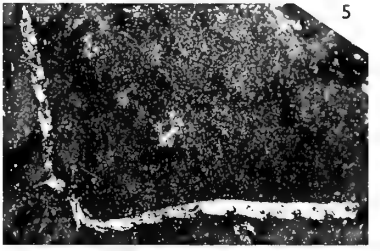

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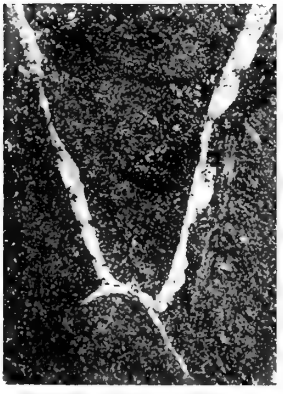

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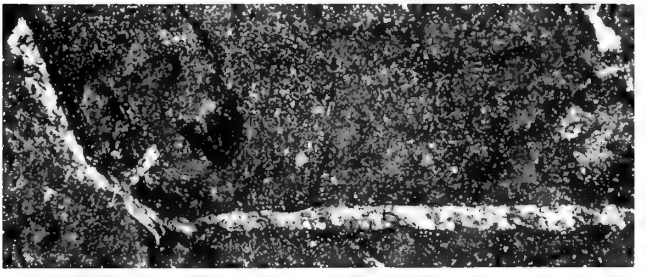


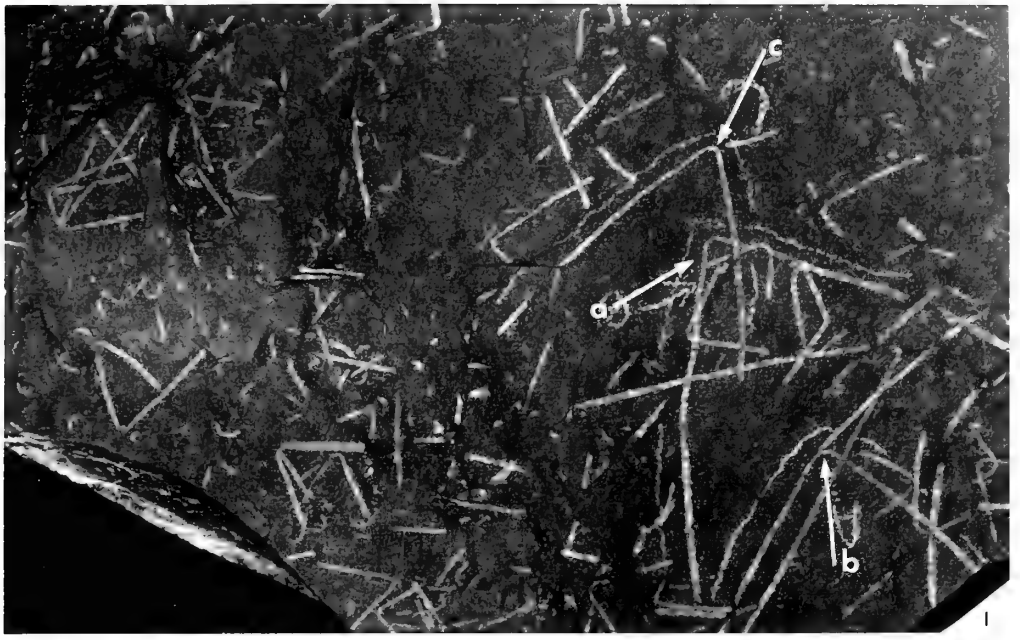
PLATE 7

Dicellograptus morrisi Hopkinson
Hartfell Shales, very top of *linearis* Zone, Dobb's Linn, Moffat, Scotland. Author's Collection.

FIG. 1. Q 2904. ×1. Associated with *D. pumilus* Lapworth.
FIG. 2. Q 2904b. ×1·5. Enlargement of FIG. 1b.
FIG. 3. Q 2904c. ×1·5. Enlargement of FIG. 1c.
FIG. 4. Q 2904a. ×1·5. Enlargement of FIG. 1a.

Dicellograptus carruthersi sp.nov.
Hartfell Shales, *linearis* Zone, Dobb's Linn, Moffat, Scotland. Author's Collection.

FIG. 5. Q 2161. ×2. Paratype, associated with *D. moffatensis*.
FIG. 6. Q 2915. ×2. Holotype.



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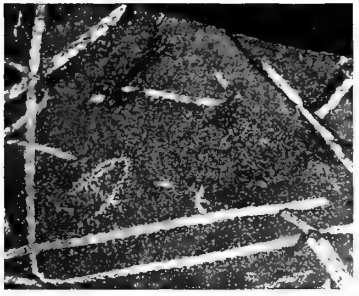

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PLATE 8

Dicellograptus moffatensis (Carruthers)
Hartfell Shales, *linearis* Zone, Dobb's Linn, Moffat, Scotland.
Q 2137, Author's Collection. ×2.

PLATE 9

Dicellograptus cf. ***elegans*** (Carruthers)
Hartfell Shales, *linearis* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 1. Q 2906. ×2.
FIG. 2. Q 2908b. ×2.

Dicellograptus cf. ***elegans rigens*** Elles & Wood
Hartfell Shales, *linearis* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 3. Q 2908c. ×2.

Dicellograptus moffatensis (Carruthers)

FIG. 4. Q 2137a. ×4. Enlargement of part of Plate 8.
FIG. 5. Q 2137b. ×4. Enlargement of part of Plate 8.

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PLATE 10

Pleurograptus linearis simplex Elles & Wood
Hartfell Shales, *linearis* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 1. Q 2972. ×4.

Pleurograptus linearis (Carruthers)
Hartfell Shales, *linearis* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 2. Q 2975. ×2.
FIG. 4. Q 2974. ×2.

Leptograptus capillaris (Carruthers)
Hartfell Shales, *linearis* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 3. Q 2950. ×1.

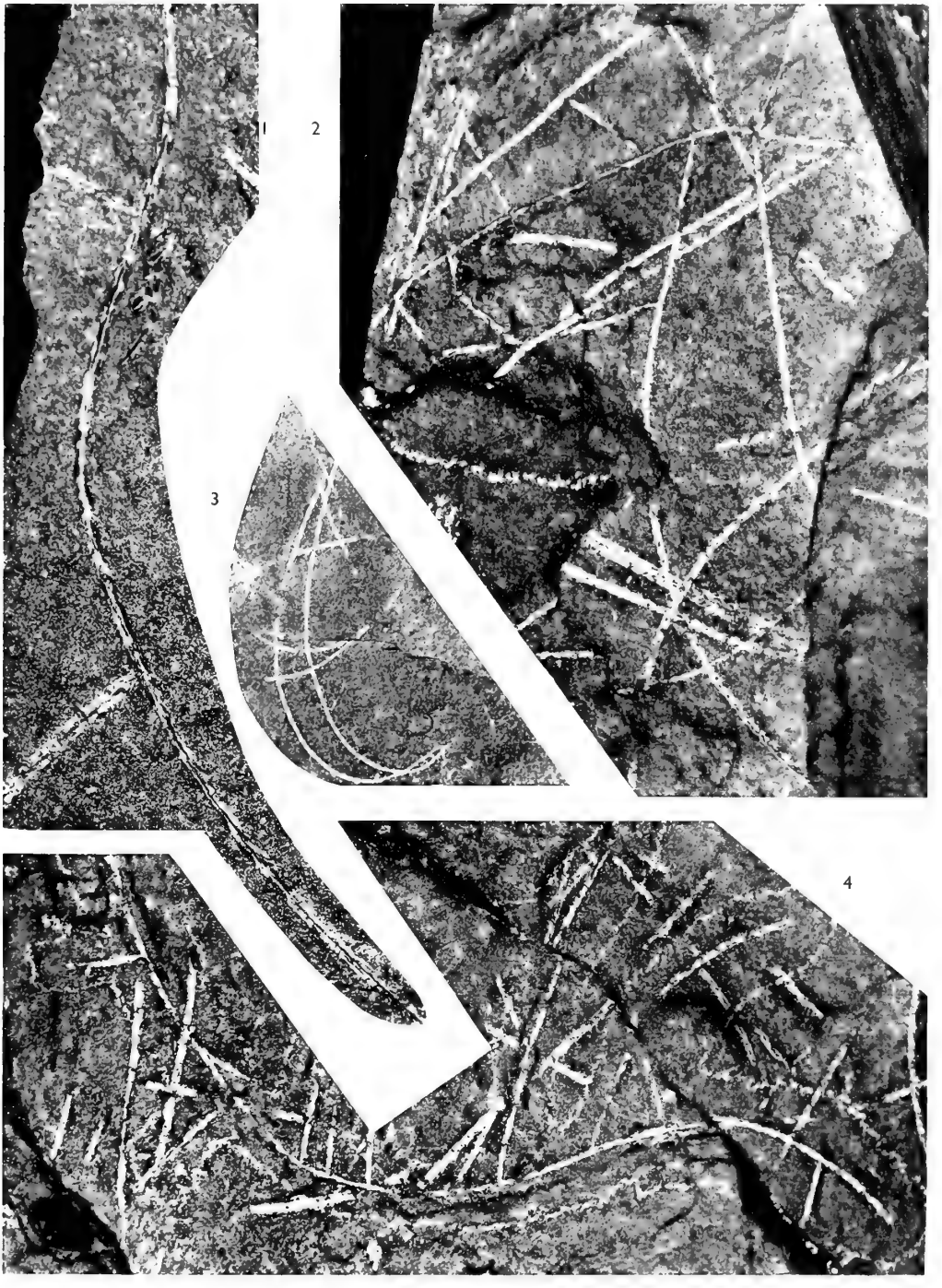
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PLATE 11

Climacograptus hvalross Ross & Berry
Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 1. Q 2787. ×5.
FIG. 2. Q 2787. ×5. Complete view of specimen in FIG. 1.
FIG. 3. Q 2830a. ×4.
FIG. 4. Q 2837. ×5.
FIG. 7. Q 2830b. ×4.

Climacograptus supernus Elles & Wood
Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 5. Q 2786. ×5.
FIG. 6. Q 2770a. ×5.
FIG. 8. Q 2773a. ×5.
FIG. 9. Q 2800. ×5.
FIG. 10. Q 2773b. ×4.

? Neurograptus sp.
Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 11. Q 2809. ×5.
FIG. 12. Q 2809. ×10. Enlargement of distal end.

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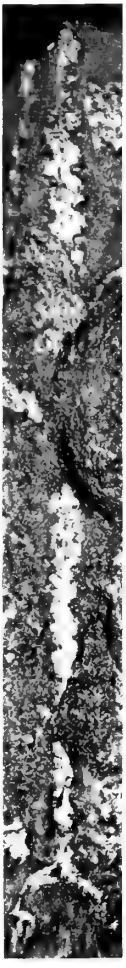

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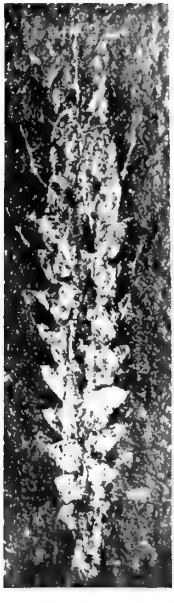

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PLATE 12

Climacograptus scalaris miserabilis Elles & Wood
Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 1. Q 2849b. ×10.
FIG. 2. Q 2867. ×5.
FIG. 4. Q 2843. ×5.
FIG. 7. Q 2838. ×10.
FIG. 8. Q 2827. ×4.
FIG. 10. Q 2850b. ×4. Counterpart of Fig. 1.

Hartfell Shales, *complanatus* Band, Dobb's Linn, Moffat.
Author's Collection.

FIG. 5. Q 2876. ×5.
FIG. 6. Q 2891. ×12.
FIG. 9. Q 2899. ×5.
FIG. 11. Q 2883. ×5.

Hartfell Shales, *linearis* Zone, Dobb's Linn, Moffat.
Author's Collection.

FIG. 3. Q 2958. ×4.

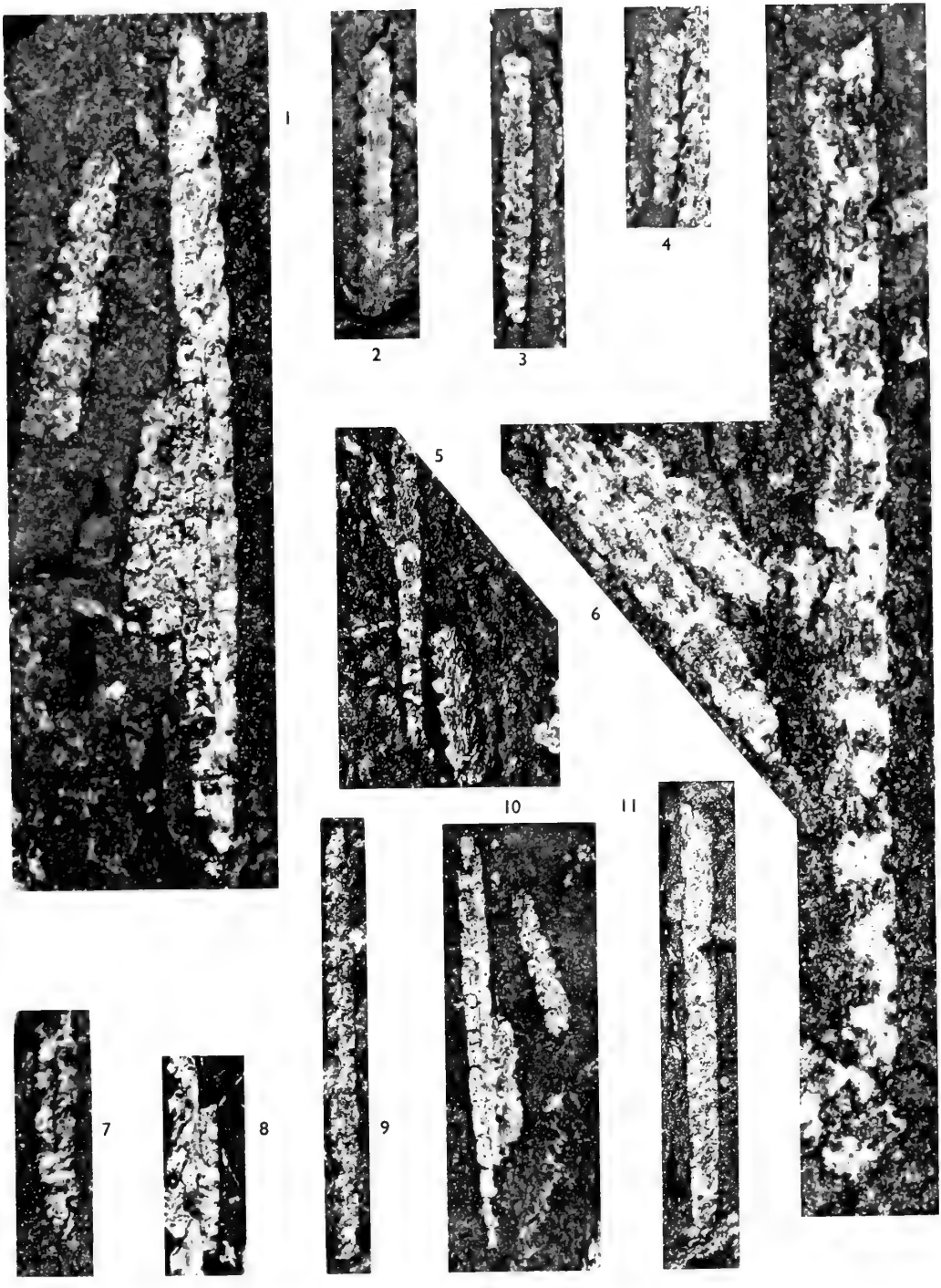
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PLATE 13

Climacograptus styloideus Elles & Wood
Hartfell Shales, *linearis* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 1. Q 2114. ×4.
FIG. 2. Q 2961. ×4.
FIG. 3. Q 2154. ×2.
FIG. 4. Q 2141. ×2.
FIG. 6. Q 2910b. ×8.

Climacograptus sp.
Hartfell Shales, *complanatus* Band, Dobb's Linn, Moffat, Scotland.
Author's Collection.

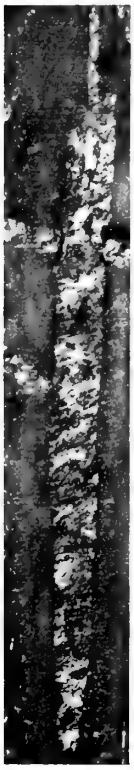
FIG. 5. Q 2903. ×5.

Orthograptus truncatus socialis (Lapworth)
Hartfell Shales, *complanatus* Band, Dobb's Linn, Moffat.
Author's Collection.

FIG. 7. Q 2877a. ×10.
FIG. 8. Q 2877a. ×5.
FIG. 9. Q 2877b. ×10.

Orthograptus quadrimucronatus (Hall)
Hartfell Shales, *linearis* Zone, Dobb's Linn, Moffat.
Author's Collection.

FIG. 10. Q 2935. ×4.
FIG. 11. Q 2934. ×4.



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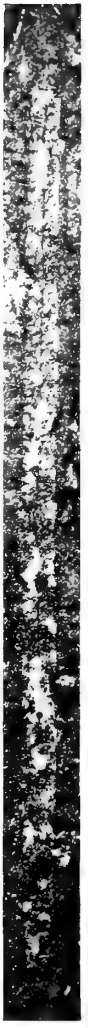

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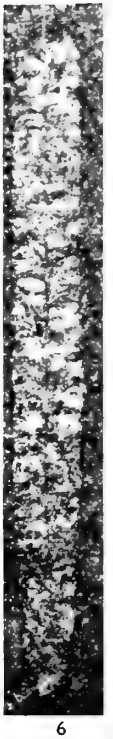

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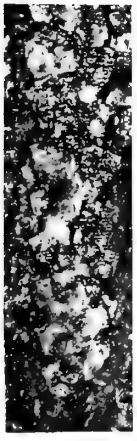

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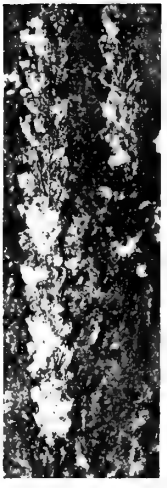

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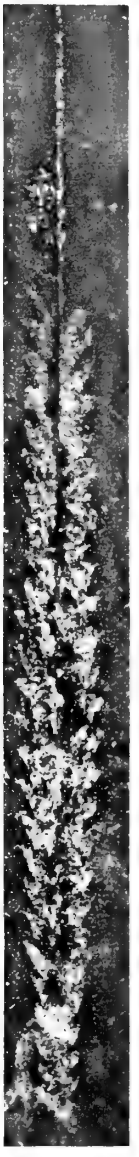

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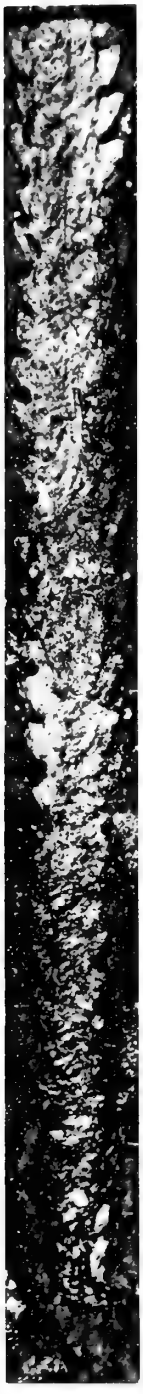
PLATE 14

Diplograptus fastigatus (Davies)
Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 1. Q 2770b. ×5.
FIG. 2. Q 2850a. ×10.
FIG. 3. Q 2851. ×5.
FIG. 4. Q 2202. ×5.
FIG. 5. Q 2759a. ×8.
FIG. 6. Q 2852. ×5.
FIG. 7. Q 2843. ×5.
FIG. 8. Q 2863. ×5. Subscalariform view.
FIG. 9. Q 2849. ×9. Distal thecae.



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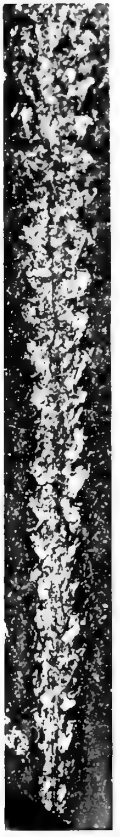

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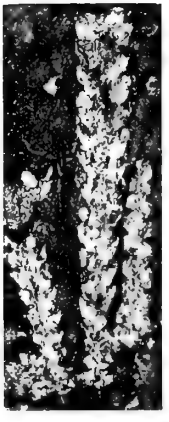

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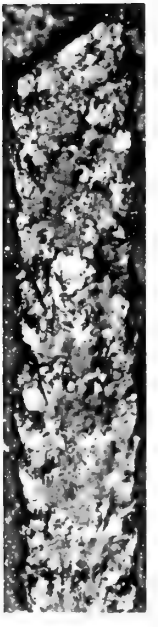

PLATE 15

Climacograptus latus Elles & Wood
Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 1. Q 2760. ×5.
FIG. 2. Q 2819a. ×4.

Glyptograptus nicholsoni sp. nov.
Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 3. Q 2767. ×8. Holotype.

Orthograptus truncatus abbreviatus Elles & Wood
Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 4. Q 2800. ×2. Associated with *Climacograptus supernus*.
FIG. 5. Q 2789. ×2.
FIG. 6. Q 2866. ×10.

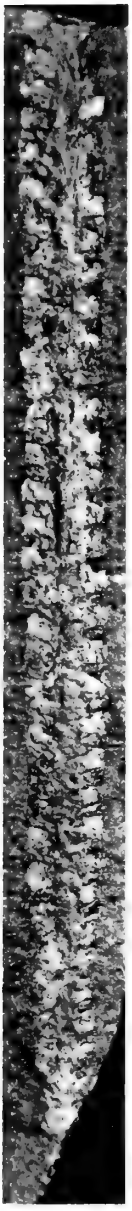

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PLATE 16

Orthograptus truncatus pauperatus Elles & Wood
Hartfell Shales, *linearis* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 1. Q 2916. ×2.
FIG. 2. Q 2910a. ×4.

Orthograptus truncatus truncatus (Lapworth)
Hartfell Shales, *linearis* Zone (Fig. 3), *anceps* Zone (Fig. 6),
Dobb's Linn, Moffat, Scotland. Author's Collection.

FIG. 3. Q 2977. ×2.
FIG. 6. Q 2790. ×2.

Orthograptus truncatus abbreviatus Elles & Wood
Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat, Scotland.
Author's Collection.

FIG. 4. Q 2804. ×5.
FIG. 5. Q 2805. ×4.

Orthograptus truncatus socialis (Lapworth)
Hartfell Shales, *anceps* Zone, Dobb's Linn, Moffat.
Author's Collection.

FIG. 7. Q 2841. ×5.

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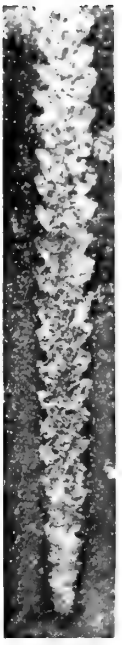

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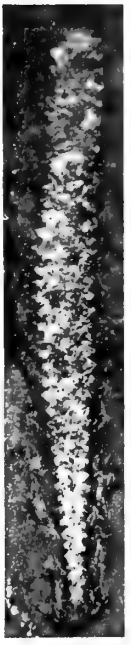

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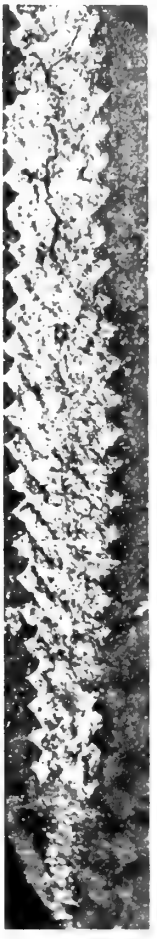

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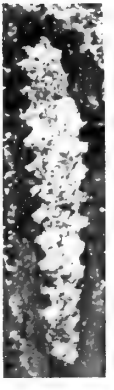

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A REVISION OF THE BRACHIOPOD SUBFAMILY KINGENINAE ELLIOTT

E. F. OWEN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 19 No. 2
LONDON: 1970

A REVISION OF THE BRACHIOPOD SUBFAMILY KINGENINAE ELLIOTT

BY

ELLIS FREDERIC OWEN

Pp. 27–83 ; 14 *Plates*, 17 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 19 No. 2
LONDON : 1970

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A REVISION OF THE BRACHIOPOD SUBFAMILY KINGENINAE ELLIOTT

By E. F. OWEN

CONTENTS

		Page
I.	Introduction	29
II.	Acknowledgments	30
III.	Techniques	31
IV.	Previous research	31
V.	Stratigraphical range and geographical distribution	32
VI.	Morphology and structure	39
VII.	Shell structure	48
VIII.	Systematic descriptions	49
IX.	Conclusions	78
X.	References	79

SYNOPSIS

This paper gives an account of previous research on the Dallinidae and comparison is made between the early loop development stages of both fossil and living representative genera.

The stratigraphical range and geographical distribution is given in fair detail with correlation tables for European, Asian and American Cretaceous horizons.

The family name Kingenidae nom. transl. for Kingeninae, Elliott 1948 is suggested and includes species of *Kingena, Zittelina* and *Belothyris*. It proposes NEOTYPES for *K. arenosa, K. mesembrina, K. lima* and *K. pentagulata* and *Belothyris pseudojurensis*. LECTOTYPES selected for *Kingena lemaniensis* and *Zittelina orbis* are redescribed in the light of present knowledge.

A new genus, *Waconella*, is erected for the North American species *wacoensis*, formerly assigned to the genus *Kingena* and now shown to be closely related to the Tertiary and Recent genus *Laqueus*.

I. INTRODUCTION

The purpose of the present research has been to investigate the early developmental stages of the brachial loop and cardinalia of certain Terebratellacean brachiopods within the Cretaceous and to show how these characters can confirm or justify the position of the genera in the classification and, at the same time, to compare and contrast the fundamental characters of mature forms and to illustrate their possible relationship to similar structures in Jurassic progenitors and Recent descendants.

The suborder Terebratellidina is divided into three superfamilies, the Cryptonellacea, Zeilleriacea and the Terebratellacea. One of the most important families within the Terebratellacea is the Dallinidae, as set out in the Treatise of Invertebrate Paleontology. The present work revises some of the genera within the family,

particularly those previously assigned to the subfamily Kingeninae. As a result of the present study, the kingenids have been raised to family level, parallel to the Dallinidae.

Apart from the well known works of Deslongchamps and Davidson in the last century and later, Muir-Wood, very little research work has been done on the Mesozoic Terebratellidina as a whole and hardly anything is known about the fossil Dallinidae in particular. Recent interest in the possible origin of this family, however, has been shown by the Russian workers Babanova and Dagis, who have illustrated early dallinoid type loop attachments in species of *Aulacothyris* from the Jurassic of the Crimea. Valuable contributions to our knowledge of the Terebratellidina have been made by the searching enquiries of these two authors but in both cases reference is made to western European species of *Aulacothyris* while their comparative material has been drawn solely from eastern European sources.

Many gaps in our knowledge of the early loop development, the vertical range and the geographical distribution of the Terebratellidina will have to be filled before any real support can be given to such drastic steps as suggested by Dagis in the taxonomic position of some of the genera he examined.

Material for this investigation has been difficult to obtain, particularly representative species of the genera *Tulipina*, *Belothyris* and *Zittelina*. It is for this reason that a more exhaustive study of species of the comparatively common genus *Kingena* has been made.

A complete monograph of the Kingeninae has not been possible as, in some cases, no comparative material has been available for further study and the original illustrations of some species has not always justified their reference to this subfamily.

II. ACKNOWLEDGMENTS

I wish to express my appreciation to the numerous people who have so kindly given me assistance during the course of this work.

I am particularly indebted to my colleagues Drs. L. R. M. Cocks and C. H. C. Brunton for their helpful suggestions and amiable company ; to the Keeper of Palaeontology British Museum (Natural History), for permission to work on the collections in his charge ; to Drs. N. J. Morris, R. P. S. Jefferies and G. F. Elliott, of the same department, for their wise counsel ; to Dr. W. J. Kennedy, Oxford University ; to Dr. Colin Forbes, Sedgwick Museum, Cambridge ; Mr. C. J. Wood, Institute of Geological Sciences ; Dr. P. J. Coleman, Department of Geology, University of Western Australia ; to Dr. Margaret Pinder for helpful discussion on Cretaceous brachiopod faunas ; to Dr. E. Lanterno, Musée d'Histoire Naturelle, Geneva ; to Mlle. Anny Dhondt, Inst. roy. Sci., Belgique, Brussels ; to Dr. W. T. Dean, Geological Survey of Canada ; to Messrs. Peter Green and Tim Parmenter, British Museum (Nat. Hist.), for most of the photographs ; to Dr. R. Goldring, University of Reading, for helpful advice and to Mr. Brian Martin and members of the staff of the Electron Microscopic Unit, British Museum (Nat. Hist.).

My very sincere thanks are due to Professor P. Allen, University of Reading, who supervised this work and who generously helped in many other ways ; to Professor Alwyn Williams for friendly discussion in the early stages of the work ; to Dr. A. J.

Rowell of the University of Kansas, and to my wife Mary, for her continued encouragement and supreme tolerance.

There are many others who have not been mentioned above and to whom I also owe my thanks.

III. TECHNIQUES

The classification of the brachiopoda depends very largely upon an intimate knowledge of the finer structures of the cardinalia and the brachial loop. In fossil genera this knowledge can be obtained in several ways. Dissection of the brachial apparatus from the surrounding matrix infilling the shell is sometimes possible providing that the matrix is sufficiently soft or is not recrystalline. Various methods have been described which make this procedure less dependent upon a high degree of technical skill. One of these is the use of an ultrasonic waterbath which removes soft matrices from brachial loops with the minimum of damage to the structures. This method has been freely used here for specimens from the Upper Chalk.

Where dissection is not possible, transverse serial sections are often used. This method described by Muir-Wood (1934), with minor modifications, has been employed for most of the specimens from either limestone or hard clay localities.

For the sake of fair comparison, this method has been used for more critical study of cardinalia and hinge structures in relation to brachidia. To aid differentiation of these characters in the case of specimens from the Upper Chalk, a technique involving the use of sugar solution described by Owen (1955) has been employed.

Where comparison has been made with Recent species, examples of dried specimens have been filled with an artificial matrix composed of plaster of Paris and asbestos powder and serial sectioned in the same way as the fossil forms.

Use has also been made of the Cambridge 'Stereoscan' electronmicroscope for the investigation of shell mosaic of both Recent and fossil species and also for the pustulate shell ornament.

IV. PREVIOUS RESEARCH

Since the publication of the Treatise on Invertebrate Paleontology (1965), the Dallinidae have become a well established family within the suborder Terebratellidina. The essential differences separating this family from other families within the suborder can best be illustrated by comparison of the very early growth stages in the development of the brachial loop.

In the Recent Terebratellidina, some of the more complex stages of metamorphosis in the ontogeny of the loop have already been described by Friele (1876, 1877), Deslongchamps (1884) and Fischer & Oehlert (1892). Basing his classification on major differences in these early stages, Beecher (1895), split off three subfamilies from the main terebratelloid group. These were the Dallininae, Magellaniinae and Megathyrinae and were later discussed and revised by Thomson (1937) who added the Platidiinae, Muhlfeldtiniae and Laqueinae. In 1940, Allan proposed the superfamily Terebratellacea with five new families, among which, the Dallinidae, had two subfamilies namely, the Dallininae and Laqueinae.

The new set of terms for the dallinoid growth stages which arose from the work of

the earlier authors was also discussed by Thomson (1927) who revised some of the nomenclature. Fischer & Oehlert (1892) had introduced the term centronelliform for the earliest loop development stage in the Dallinids ; Beecher (1895) replaced this term by platidiform in his classification. This was once again replaced by Thomson (1927) who used the term pre-ismeniform for this early stage. A further correction was made by Elliott (1947) who pointed out that the loop in *Ismenia pectunculoides* (Schlotheim), the type species of *Ismenia* from the Upper Jurassic of Germany, does not correspond with what is known as ismeniform stage of loop development of the Recent Dallinids and proposed the alternative names of pre-campagiform and campagiform from the Recent genus *Campages* to replace the terms pre-ismeniform and is meniform as used by Thomson (1927).

Most of the terminology and classification surrounding the dallinoid brachiopods, therefore, has been developed from the study of Recent genera. Comparatively little is known about the Mesozoic Dallinidae and little advance has been made on the work of earlier authors such as Deslongchamps and Fischer & Oehlert.

Over the past twenty years, however, further contributions to the classification have been made by Elliott (1947) who described the genus *Gemmarcula* from the Lower Cretaceous, Upper Aptian of Faringdon, Berkshire, illustrating his description with a series of carefully prepared dissections of early dallinoid brachial loop stages. For this genus Elliott proposed the subfamily Gemmarculinae.

Later Elliott (1948) described and illustrated a series of early loop stages in the genus *Hamptonina* from the Great Oolite of Hampton Down, Bath. These show the pre-campagiform and campagiform stages to perfection and the specimens are again used in the present work, Pl. 11, figs. 1–3, for comparison with early growth stages in the brachial loops of specimens of *Kingena* from the Upper Chalk.

In 1948, in a paper discussing the evolutionary significance of the brachial development of terebratelloid brachiopoda, Elliott proposed the subfamily name of Kingeninae for the Cretaceous genus *Kingena* Davidson, 1852. To this has been added *Zittelina*, erected by Rollier (1919) for *Terebratula orbis* Quenstedt (1871) from the Upper Jurassic of Wurttemburg, Germany ; *Belothyris*, described by Smirnova (1960) from the Lower Cretaceous of the southern Caucasus and *Tulipina* which Smirnova (1962) described from the Lower Aptian of Georgia.

The proposal of a new subfamily, Belothyrinae for the genus *Belothyris* was made by Smirnova (1960) but this was not adopted by Elliott in preparation of the section on Dallinidae for the Treatise on Invertebrate Paleontology (1965).

Further details concerning the relationship of the above genera and a comparison of internal structures in both Recent and fossil representative species of the Dallinidae is given in the foregoing sections on Morphology and Structure and in the Systematic Descriptions of the present work.

V. STRATIGRAPHICAL RANGE AND GEOGRAPHICAL DISTRIBUTION

The accepted stratigraphical range for the subfamily Kingeninae is that quoted in the " Treatise " (1965) as Upper Jurassic to Cretaceous. Of the four genera so far included in the subfamily, the genus *Zittelina* of Rollier (1919), occurs in the Upper Jurassic, Weiss Jura of Wurttemburg, Germany from whence the type species,

Terebratula orbis Quenstedt (1858), was originally described. This genus also occurs in the hard limestone facies of the Tithonian of Stramberg, the " Stramberger-Schichten " of Czechoslovakia and from a similar horizon at Gard and Herault, France. In 1905, Krumbeck extended the distribution of the genus to the eastern Mediterranean, describing two new species, *Z. latifrons* and *Z. triangularis*, and recognizing three of Quenstedt's species, *Z. orbis*, *Z. gutta* and *Z. cubica* from the Upper Jurassic of the Lebanon. He mistakenly referred these to the Cretaceous genus *Kingena*, but they are here referred to the genus *Zittelina*.

The genus *Belothyris* was described by Smirnova (1960) from the Lower Cretaceous of northwest Caucasus. Examples of topotype material of three species, *B. plana*, the type species, *B. regularis* and *B. marianoviensis* have been kindly presented to the British Museum (Natural History) by Dr. Smirnova and are figured here Pl. 10, figs. 3, 4 & 5. These specimens have been used for comparison with specimens collected from the Lower Cretaceous of Sheik Budin, southeast of Pezu, N. W. Frontier Province, Pakistan. The comparison is favourable and establishes, without doubt, that the two forms are congeneric, but more material from both Russian and Pakistani localities is needed before any realistic comparison of species can be made.

In her original description of the genus *Belothyris*, Smirnova suggested that " *Zeil leria* " *pseudojurensis* described by Leymerie (1842 : 12) from the Hauterivian of Marolles (Aube), France, might belong to her genus. As a result of her suggestion, an investigation of Leymerie's species *pseudojurensis* has been carried out during the course of the present research with the result that this species can now be referred to the genus *Belothyris* Smirnova.

Belothyris pseudojurensis (Leymerie) is widely quoted from Neocomian beds in France and Switzerland, occurring in the *radiatus* Zone of the Lower Hauterivian at Le Landeron, and Neuchâtel, Switzerland and from the type locality, Marolles and from Auxerres (Yonne), Vendeuvre and Avalleur, France.

No duplicate specimens of *Tulipina* which Smirnova (1962) described from the Lower Aptian of Georgia have been obtained for the present study but passing reference is made to the internal characters of the type species, *Terebratula koutaisensis* de Loriol from the Hauterivian of Switzerland and is discussed in the section on Morphology.

Although the geographical distribution of the Kingeninae can be quoted as world-wide, the records show this to be due in the main to citations of the Cretaceous genus *Kingena*. Not all the records appear to be authentic, but where possible, duplicate material has been obtained and studied and is either referred to or figured here.

European records of *Kingena* are chiefly from British, Belgian, French and German localities. In France, the type species *Terebratula lima* was originally described by Defrance (1828) from an undoubted Upper Chalk locality in the Beauvais district of Normandy. Unfortunately, no specimen identified as *T. lima* by that author has survived and the vague reference to " craie de Beauvais " has led to somewhat wild speculation as to its stratigraphical position. In addition to Defrance's description, d'Orbigny (1847 : 108) described a specimen from the Upper Senonian of Chavot, (Marne), as *Terebratula hebertiana*. This species is regarded here as a synonym of

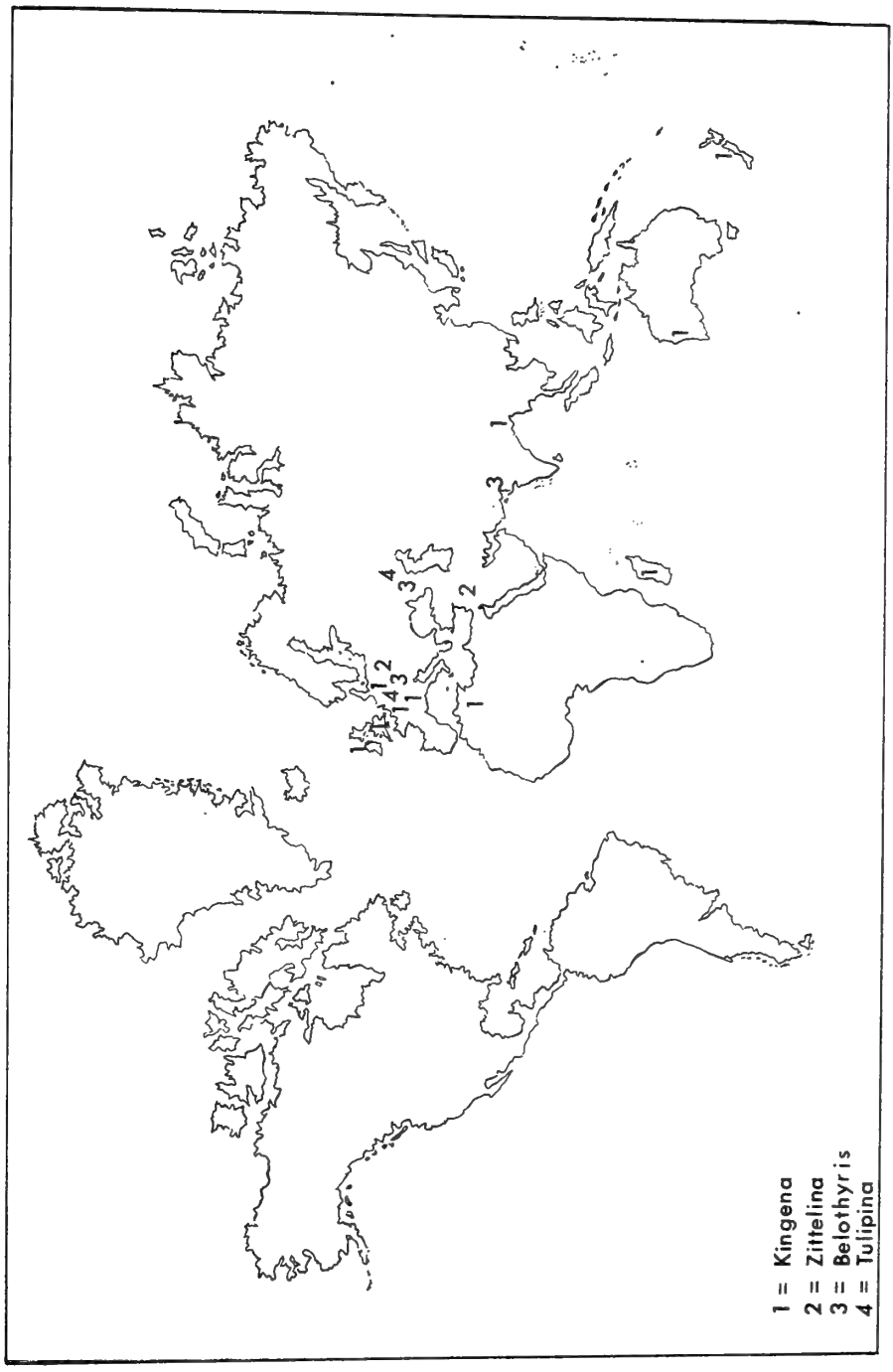


FIG. 1. Sketch-map showing global distribution of the Kingenidae.

Woodward's *Kingena pentangulata* described from the Upper Senonian, *Belemnitella mucronata* Zone of Norfolk in 1833.

d'Orbigny made further reference to a species of *Kingena* in the same publication (1847 : 98, pl. 512. fig. 1–5) with his description of *Terebratula lima* which he quoted from the Cenomanian of Le Hâvre. This reference is discussed under the description of *Kingena arenosa* (d'Archaic) p. 55, to which species d'Orbigny's specimen has been assigned.

In Belgium, species of *Kingena* have been quoted from Cenomanian localities in the districts of Tournai and Montignies-sur-Roc, d'Archaic having described *Kingena* from the Tourtia of Gussignies.

From the Upper Chalk of the Mons and Ciply districts, two species are comparatively common fossils. *Kingena blackmorei* sp. nov. occurs in the Craie de Trivières at approximately the same horizon as the *Gonioteuthis quadrata* Zone in Wiltshire from which it was originally collected and is probably present in the base of the Craie d'Obourg. It certainly occurs in the conglomerates which separate the two beds and are known as Conglomerats d'Obourg.

By far the commonest species of *Kingena* occurring in the Belgian Upper Chalk is the British species *Kingena pentangulata* (Woodward) which occurs at Harmignies in the Craie de Nouvelles and at Obourg in the Craie de Spiennes and Craie d'Obourg (see Table 1 p. 36).

German records, on the other hand, are not so plentiful, being those of Geinitz (1850) and Schloenbach (1866, 1867, 1868) for species from the Middle and Upper Chalk of Westphalia.

Roemer (1840) described and figured many brachiopods from various horizons within the Cretaceous of north Germany. Among these, *Kingena pectoralis* from the Hilsconglomerat near Essen, was described (p. 42) and figured (pl. 7, fig. 19 a, b, c.) as *Terebratula pectoralis*. The term Hilsconglomerat, as used by Roemer (1840) can be interpreted to cover beds ranging in age from Lower Noecomian to Cenomanian (see Stolley, 1908). Roemer's specimen could have come from any one of those horizons. Furthermore, the specimen figured by Roemer on pl. 7 is shown as an elongate-pentagonal specimen which could very well have orignated from the Albian or Cenomanian. The species *Kingena pectoralis* (Roemer) is, therefore, regarded here as *nomen dubium*.

Outside Europe, records of *Kingena* extend to Greenland, Canada, north and south America, Madagascar, Africa, southern India, Tibet and Australia.

Of these records, not all are reliable. The species described by Frebold (1935) as *Kingena groenlandica* from the Aptian of East Greenland is not referable to this genus. As figured and described by Frebold, it shows none of the diagnostic characters of the genus and may possibly belong to *Tamarella* Owen 1965.

The species described by Whiteaves (1903) as *Kingena occidentalis* from the Upper Chalk of Canada, bears only a superficial resemblance to the genus and must be left in doubt until more material from this locality is available. The short septum and lack of any obvious dental plates suggests a possible relationship with a terebratellid recently described as *Kingenella* from the Maastrichtian of Poland by Ewa Popiel-Barczyk (1968).

TABLE I

STAGE		Southern England	Northern Ireland	Belemnite Horizons	Norfolk	Western Belgium
LOWER MAASTRICHTIAN		Not represented	Ballycastle White limestone	Belemnella occidentalis	Grey Beds Liostrea lunata Beds Sponge Beds	Craie de Ciply
				B. lanceolata	Porosphaera Beds Preporosphaera Bed	Craie de Spiennes
				Belemnitella langei dominant	Paramoudra chalk	
					Beeston Chalk	
SENONIAN Pars.	Upper Campanian		White limestone	Belemnitella mucronata minor and allied forms	Catton Sponge Bed Weybourne Chalk	Craie de Nouvelles Craie d'Obourg
		Highest chalk of Isle of Wight and Dorset coast. B. mucronata Zone Base of zone in Hants.			Eaton Chalk	
				B. mucronata sens. str.	Basal Mucronata Chalk	Conglomerat d'Obourg
	Lower Campanian	G. quadrata Zone		Gonioteuthis quadrata	Gonioteuthis Zone	Craie de Trivière

Showing correlation of British and western Belgian Upper Chalk beds. (Taken partly from Peake & Hancock 1961).

References to *Kingena wacoensis* (Roemer), which was originally described by F. Roemer (1852 : 81) from the Lower Cretaceous of Texas, U.S.A., have been numerous and quotations of this species frequently appear in faunal lists of Lower Cretaceous fossils from Mid West and southwestern localities of Central U.S.A. and from Mexico.

Although this species is already well entrenched in American literature under the generic title of *Kingena*, recent investigation of this form in preparation for the present work has revealed that it belongs to a completely different generic stock from *Kingena* and is described here as *Waconella* gen. nov. Lack of plentiful material from all the known localities and horizons has prevented a thorough investigation of the genus but it is hoped in future to follow up this study with further investigations of a more concentrated nature.

The occurrence of *Waconella wacoensis* (Roemer) in the Comanchean Series is discussed under the description of the genus but a correlation table, Table 3 p. 40, is included here to give some guide as to the relative age of the beds in terms of European stratigraphy.

Richter (1925) referred a brachiopod from the Upper Cretaceous of Tierra del Fuego, Chile, South America, to *Kingena lima* but the specimens he figured (pl. 9, figs. 31, 32) show the internal moulds of a small cuboidal brachiopod species with a short median septum and carinae bordering a shallow sulcus on the brachial valve. It is a fragmentary specimen with a small incurved umbo and minute foramen and is almost certainly not referable to the genus *Kingena*.

African records are those of Ficheur (1900) who recorded *Terebratula lemaniensis* Pictet & Roux, here referred to *Kingena*, from the Lower Albian of Algeria and Drot (1953) who referred to a *Kingena* species from the Cenomanian of Tunisia.

In addition, Müller in Bornhardt (1900) described *Kingena schweinfurthi* from the Lower Cretaceous of Ntandi, Tanzania but, to judge from the specimen which he figured (pl. 25, fig. 11), the species would appear to belong to some genus other than *Kingena*. The beak characters show a small foramen in a slightly produced suberect umbo with no obvious sign of beak-ridges. No reference is made in the description (p. 548) to external ornament and the figured specimen is seemingly without a clearly marked median septum in the brachial valve. Although the whereabouts of Müller's specimen are not known, the species occurs in beds containing "*Trigonia*" *swartzi* Müller (see Aitken 1956) which has a limited range of Valanginian to Lower Aptian age. It is conceivable that Müller's specimen may be referable to the genus *Belothyris* from the Hauterivian.

Collignon (1950 : 28) referred a specimen collected from the Albian of Madagascar to *Kingena asperulina* Stoliczka which was originally described (Stoliczka, 1872) from the Utatur beds of Southern India. The specimen which Collignon figured (pl. 3, figs. 15 a, b.) certainly bears more than a superficial resemblance to the specimen figured by Stoliczka (pl. 7, fig. 14) and these forms may well be conspecific. The age of the Utatur beds is given as Upper Albian to Cenomanian in the Lexique Stratigraphique International (see Table 2 p. 38).

Sahni (1939 : 11) considered that the specimen which he described and figured (pl. 1, figs. 4, 5) from the Pezu district, Pakistan, should be referred to *Kingena*,

although he admitted that it showed no evidence of pustulate ornament of the shell. It is quite likely that *K. punjabica* belongs to another genus, possibly *Belothyris*, but the information regarding its exact stratigraphical origin is vague.

The reference by Muir-Wood (1930 : 34) to two species, *K. spinulosa* (Davidson & Morris) and *K. tumida* Muir-Wood to the Gault of the Samana Range increases the geographical range of Albian records of the genus to India.

Spengler (1923, pl. 1, fig. 13 a, b, & 14) described and figured a crushed specimen under the name of *Waldheimia* species from the Upper Chalk of Tharia Ghat, Assam. The specimen figured by Spengler bears a distinct resemblance to *Kingena blackmorei* sp. nov. from the *Gonioteuthis* Zone of Wiltshire.

TABLE 2

EUROPEAN STAGE		
DANIAN	ARRYALUR GROUP	
MAASTRICHTIAN		
CAMPANIAN		
SANTONIAN	TRICHINOPOLY GROUP	
CONIANCIAN		
TURONIAN		
CENOMANIAN	UTATUR GROUP	
Ur. ALBIAN		

Rough correlation of Cretaceous Beds of Southern India with European stages

It is probable that the specimen described by Douvillé (1916) from the Maastrichtian of Tibet as *Kingena hebertiana* d'Orbigny is an undescribed or new form. It may, however, be referable to *K. shalanurensis* Stoliczka from the Arryalur beds of Southern India.

Further records of *Kingena* from India were made by Stoliczka (1872) who, apart from K. *granulifera* mentioned above, described two further species namely, *K. asperulina* from the Utatur group and *K. shalanurensis* from the ? Trichinopoly group. These forms are described and discussed briefly in the systematic section here.

Etheridge's citation of *Magas mesembrinus* from the Upper Cretaceous of Western Australia was discussed and revised by Elliott (1952) in a description of some of the brachiopods from the Gingin Chalk who referred the species to the genus *Kingena*.

The age of the Gingin Chalk has been the subject of much discussion over the past fifty years and Glauert (1910, 1926) gave a good general account of its position at that time. Withers (1924, 1926), following the discovery of the crinoids *Uintacrinus* and *Marsupites*, pointed out that these fossils occur as horizon markers in the Upper Cretaceous of Western Europe. More recently McWhae, Playford, Lindner, Glenister and Balme (1958) and Belford (1958) have discussed the position of the Gingin Chalk and the Toolonga calcilutite in relation to microfaunas, particularly of ostracoda.

An unpublished record of a Kingenoid brachiopod is from the Upper Cretaceous of New Zealand where specimens of an undescribed species have been collected from the

beds cropping out at a stream section in the district of Koranga, North Island. Specimens obtained by collectors in the Geological Survey of New Zealand have been examined (locality nos. 5792, 1401) and appear in a dark-grey, highly glauconitic, coarse sandstone with *Ostrea lapillicota*. According to Wellman (1959 : 138, 149) this fossil serves as a marker in the Lower Haumurian beds of Maastrichtian equivalent.

Outside the Cretaceous, reference to three fossil examples of *Kingena* and one from Recent seas have been made. Of these, *K. raincourti* was described by Deslongchamps (1863 : 294) from the Eocene, Calcaire Grossier, of Paris basin. From the illustrations of the specimen figured by Deslongchamps (pl. 8, figs. 12–14) fine pustules or granules are seen on the shell surface but, apart from this feature, there is little to commend its reference to the genus *Kingena*. In the same way, the specimen described and figured by Cossman & Pissaro as *K. constantinensis* (1904 : 31, pl. 19, figs. 29, 30) from the Eocene of the Cotontin, France, is probably not referable to *Kingena*.

Likewise, the reference to *Kingena simiensis* by Waring (1917 : 73) from the Eocene of Simi Hill, Ventura County, California, U.S.A. is also likely to belong to some other genus.

A Recent form from the Indian Ocean described by Joubin (1906) as ? *Kingena alcocki* has been referred by Dall (1920) and Jackson (1921) to the genus *Frenulina* but it is more likely that it has closer affinities to *Laqueus*. An example of "*Kingena*" *alcocki* (Joubin) is figured here, Pl. 12, figs. 3 & 4, for comparison with *Waconella* gen. nov. with which it appears to have much in common. It is also used to illustrate the different mode of attachment of brachial loop to median septum from that seen in the Kingeninae.

VI. MORPHOLOGY AND STRUCTURE

The terms used in the description of the characters, both generic and specific, throughout this work are those found in the glossary of morphological terms in the Treatise on Invertebrate Paleontology (1965).

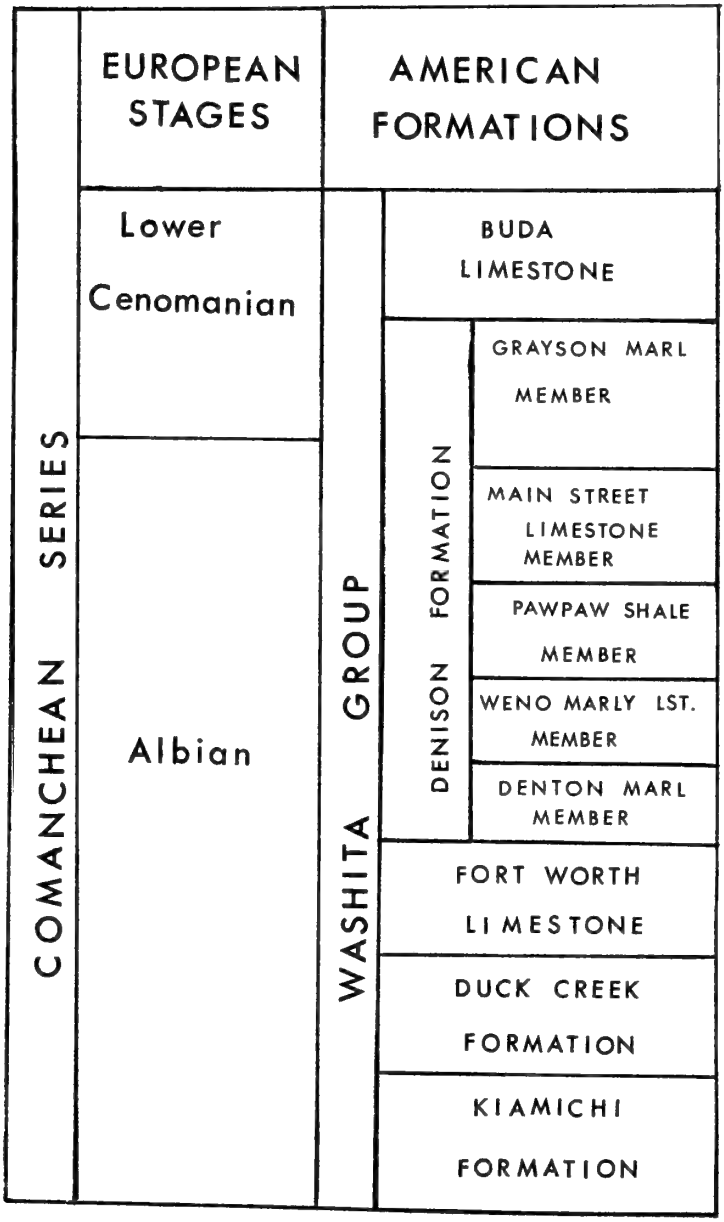
Special reference is made in the systematic descriptions to terms applied to characters observed from transverse serial sections representing species examined or from dissected and acid developed specimens. Any reference to characters seen in "Stereoscan" micrographs or in thin longitudinal sections or transverse shell sections has been stated in the legend to the illustrations.

External morphology. The general outline of the four genera at present represented by the subfamily Kingeninae is oval-pentagonal to pentagonal. The term pentagonal, in this instance, being comparable to "spade-like" with the broadest end of the spade representing the posterior part of the brachiopod.

Within this rather restricted morphological range, certain distinct features can be recognized and are discussed in broad outline in this section, but are dealt with in greater detail under the description of each genus. In the same way, the more subtle details which allow the genera to be separated into species, are discussed more fully in the systematic section.

The general morphological pattern for both *Zittelina* and *Kingena* is very much the

TABLE 3



Correlation of the beds of the Washita Group of Texas and Mexico with the main European stages, Albian and Cenomanian.

same. Both genera pass through a similar ontogenetic series of outlines. These begin with subcircular, becoming broadly-oval and passing to elongate-oval to pentagonal.

The appearance of the shell surface depends largely upon the mode of preservation, but it is noticeable that in some species, particularly of *Kingena*, the concentric growth-lines are very much more prominent.

Ornamentation of the shell surface in the Terebratellacea usually manifests itself in the form of strong bifurcating or non-bifurcating radial costae and striae. Some shells, however, remain free of additional ornament and have a smooth shell surface on which can be seen the pattern of punctae. *Kingena*, unlike all other Terebratellacean brachiopods, retains a shell surface ornament of evenly distributed spinose pustules or granules from its earliest developmental stages to adult form. Although this pustulate or granular ornament appears to have no parallel in either Recent or fossil genera, comparison has been made with forms which exhibit protuberances or outgrowths of primary or secondary shell layers.

Pustulate or spinulose external ornamentation of the shells of Productida and Spiriferida is a common enough character in Middle and Upper Palaeozoic genera, but it is rarely found in the Terebratulida. In the Mesozoic, however, examples of ornament similar in some respects to that of *Kingena* exists on the surface of some genera. In particular, the genus *Pseudokingena*, described by Böse & Schlosser (1900) for Davidson's *Terebratula deslongchampsi* from the Middle Lias of Normandy, exhibits an apparently similar shell surface ornament to that of *Kingena* and is in some ways comparable. Representative specimens of this genus are extremely rare but, from the few examples examined, it seems possible that *Pseudokingena* might represent an early stage in the ontogeny of a Terebratellid rather than with the Terebratulids with which it is at present classified (Muir-Wood 1965 : H 772).

In some very young stages of Recent Dallinidae an ornament of comparatively large rounded granules has been noted. Deslongchamps (1884, pl. 13, figs. 13, 14) illustrated this ornament in a series of young stages of *Macandrevia cranium* (Muller). It would appear that this type of ornament does not survive into the adult developmental stages of the shell as there is no evidence of any such ornament found on mature shells of this genus.

A "tear-drop" type of ornament appears on the surface of "*Terebratula*" *ovata* (J. de C. Sowerby) and "*T.*" *arcuata* (Roemer) from the Cenomanian of English and German localities. Davidson (1852, pl. 4, figs. 11c & 14c) figured an enlargement of this ornament on a specimen of "*T.*" *ovata* from the Cenomanian of Warminster, Wiltshire. This type of ornament differs from that of *Kingena* in its shape and distribution. The "tear-drop" or pear-shaped pustules are arranged in rows, almost equally spaced and occurring on the shell surface exposed between the numerous prominent growth-lines as though they were originally just peripheral ornament on the leading or growing edge of the shell.

In the longitudinal tangential sections of the shell of a specimen of *Kingena pentangulata* (Woodward) from the Upper Chalk of Norfolk, shown here Pl. 13, figs. 5 & 6, it will be seen that the pustulate ornament consists of a conical outgrowth of the primary shell layer which does not influence nor is influenced by the underlying

secondary shell layers. It differs from the spines or spinules found on the surface of some Productida and Rhynchonellida in that it is entirely composed of solid shell matter and is not a hollow structure penetrating the shell (Williams & Rowell 1965 : H 85).

Specimens of *Kingena spinulosa* (Davidson & Morris) which have been examined in preparation for this work, appear to have a somewhat distinct pustulate ornament. Although they do not differ in structure from the pustules on the surface of other species of *Kingena*, they consist of both large and small conical outgrowths and are indiscriminately distributed over the shell surface, the smaller pustules appearing between the larger.

Tubercles on the inner surface of the shells of some Recent Terebratellida are in complete contrast to the structures described on the shell surface of *Kingena*. They are, in some ways, more comparable to the pseudopunctae seen in the strophomenoid shell (Williams & Rowell 1965 : H. 71) where outgrowths of secondary shell appear on the inner surface of the valve. The tubercles of the Terebratellida, mentioned above, are seen to have a deep underlying influence on the secondary layers in very much the same way as do the pseudopunctae.

The umbonal features of the Kingeninae are of specific importance and may present some evidence of change of environment. A large foramen truncating a massive umbo is almost certainly developed as a result of the need for increased pedicle support. Such support would be necessary in more disturbed or turbulent waters and this character is noted more frequently on species collected from beds exhibiting other signs of turbulence. At Wilmington, south Devon, current bedding is a common feature of the loose sandy facies of the Cenomanian which yields numerous specimens of *Kingena arenosa* (d'Archaic), a species with a large foramen truncating a massive umbo. The same type of umbonal characters are noted in the species *Kingena blackmorei* sp. nov., Pl. 14, fig. 4, from the Upper Senonian, *Gonioteuthis* zone of Wiltshire and Hampshire.

A slightly produced, rounded, dome-like umbo is a character more commonly found in the Middle and Upper Chalk species, Pl. 14, figs. 1 & 2. Both *Kingena elegans* sp. nov. from the Turonian and *K. pentangulata* (Woodward) from the Upper Senonian are characterized by this strong specific feature. In the case of the Turonian form, the foramen is small and circular and the beak-ridges indistinct or smooth. A short interarea is developed and disjunct deltidial plates are exposed.

In *Kingena pentangulata*, the same dome-like umbo is developed, but there is a strong tendency to labiation of the foramen and the interarea is extremely short, allowing little or no exposure of the deltidial plates, Pl. 14, fig. 1.

Apart from the external pustulate ornament of *Kingena*, the general account of the morphology of the genus, given here, might very well be applied to *Zittelina* from the Upper Jurassic of Germany. The characteristic pentagonal outline prevailing throughout the subfamily is the dominant feature of the general outline of the type species, *Zittelina orbis* (Quenstedt). Variation extends to slightly more quadrate and subcircular plan. The genus does not show any marked tendency towards elongation, as is noted in most species of *Kingena* described here. Anterior sulcation of both brachial and pedicle valves is slight and is usually bordered by faint carinae.

The umbo in *Zittelina* is slightly incurved, but the interarea is extensive in most species and marked by sharp, or distinct, permesothyrid beak-ridges. The foramen in all species remains circular and is medium to small in size.

The genus *Belothyris* is represented by five species, four of which Smirnova (1960) described from the Lower Cretaceous of the Northwest Caucasus. The fifth species, *B. pseudojurensis* was originally described by Leymerie (1842) as *Terebratula pseudojurensis* from the Neocomian of Marolles, France, and is referred here to the genus *Belothyris* Smirnova 1960.

The genus varies in outline from distinctly elongate-pentagonal to elongate-oval. The type species *B. plana* Smirnova, is broad, flat and somewhat zeilleriform or cinctiform in general outline. An anterior sulcus is fairly well marked in both valves, giving rise to a ligate anterior commissure. The hinge-line is narrow and the shoulders of the umbo are steep with an acute apical angle. The small circular foramen is bordered by permesothyrid beak-ridges.

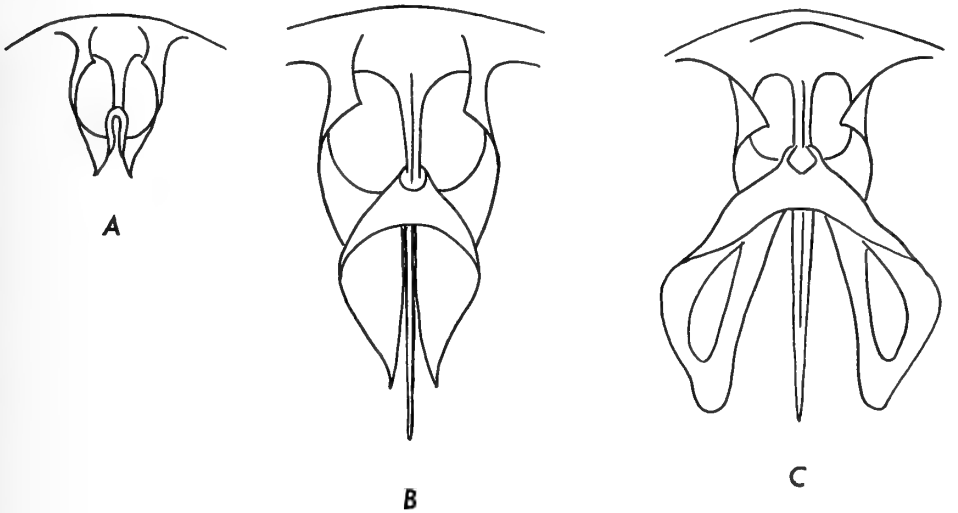


FIG. 2. Diagram illustrating the three stages in the loop developments of *Kingena* and *Zittelina*.
(A) Precampagiform. (B) Early campagiform.
(C) Mature kingeniform.

As no specimens of the genus *Tulipina* Smirnova, 1962 have been obtained for the present study, nothing can be added to the original description of the genus (Smirnova 1962 : 102).

Internal characters. Although the two genera *Zittelina* and *Kingena* have many external morphological features in common, this is not to say that the two forms are in any way more closely related than any other genera investigated here. With such a list of characters in common, and bearing in mind their stratigraphical relationship, it would seem logical to suppose that *Zittelina* was the direct ancestor to *Kingena*,

although investigation of the Hauterivian genus *Belothyris*, carried out here, throws light on an alternative evolutionary trend and a possible link with Lower Albian species now considered to belong to the genus *Kingena*. There are still many gaps in our knowledge of these forms and more research is needed before any hard and fast conclusions can be reached as to their lineage.

The internal characters of both *Zittelina* and *Kingena* are broadly discussed and compared here.

Both genera have similar cardinalia, consisting of a very small cardinal process, with deep concave hinge-trough supported by long, high median septum. The descending branches of the brachial loop, originating from the distal ends of the hinge-trough, extend anteriorly, developing long crural processes. Attachment of the descending branches to the septum is by means of two broad bands, one from either branch, which curve inwards towards the septum and then upwards and outwards,

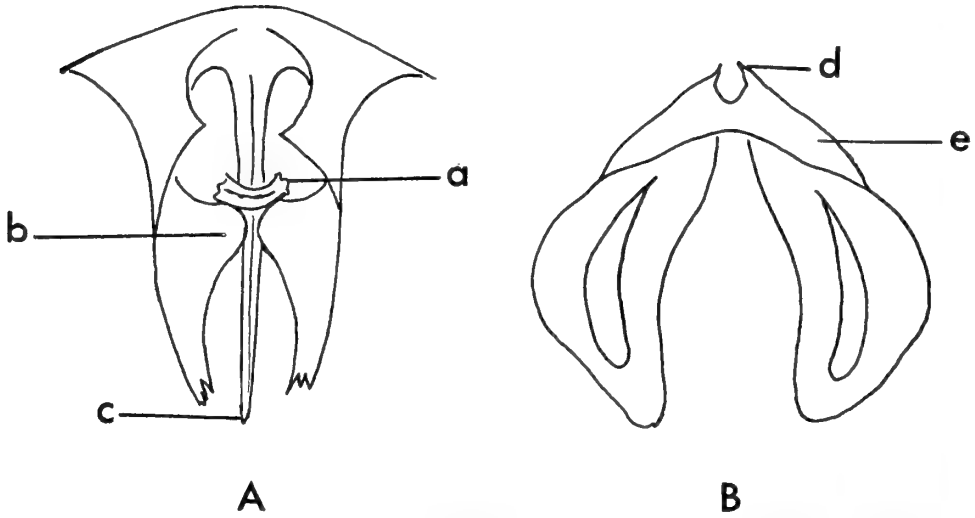


FIG. 3. A. Descending branches of *Kingena* showing a. points of connection to kingeniform hood. b. broad transverse bands to septum. c. long median septum. B. Kingeniform hood showing d. extensions for connection with median spetum. e. broad conical expanded band or hood.

describing a low arc or semicircle, to form a connection for the extended ends of the broad transverse band or conical kingeniform hood of the ascending branches, Fig. 3. These fuse with a thickened part of the edge of the median septum at this point.

The ascending and descending branches are broad, somewhat resembling those of *Campages*, but are separated by extensive lateral lacunae. These lacunae tend to be more highly developed in *Kingena* than in *Zittelina*.

In the Recent genera *Frenulina* and *Laqueus* which have a similar loop development to that of *Kingena* and *Zittelina*, the brachidia are developed at a more anterior

position in the shell and appear to reach maturity at a later stage than in the fossil genera. *Kingena* and *Zittelina* both have a mature loop developed at a very early stage in their ontogeny.

Although lack of suitable young forms prevents a thorough investigation of the growth stages in *Zittelina*, it would seem from the examination of transverse serial sections of mature individuals that the main differences between *Zittelina* and *Kingena* lie in the development of the transverse band or hood, which appears to be less conical or more quadrate in tranverse outline in *Zittelina* than in *Kingena*, and in the descending branches being placed at a more acute angle in relation to the central septal pillar. In transverse serial sections of the descending branches of *Kingena*, they are seen to lie almost at right-angles to the septum, except in the very early growth-stages.

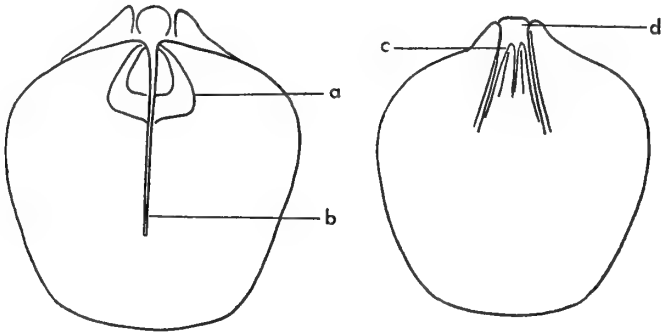


FIG. 4. Impressions of adductor and diductor muscle-scars on an internal mould of *Kingena spinulosa* (Dav. & Morris) from the Cambridge Greensand. a. adductor scars. b. impression of septum. c. adductor and diductor muscle-scars in pedicle valve. d. umbonal cavity in pedicle valve.

In *Belothyris*, the median septum is almost as proportionately long as in *Zittelina* and *Kingena*, but is higher in its development from the floor of the brachial valve. No direct or indirect attachment is made from the septum to the descending branches. The hood, almost triangular in transverse section, is approximately conical in general shape and develops later or at a more anterior position in the valve than in either *Kingena* or *Zittelina*. The general plan of the mature brachial loop, as seen in transverse sections, Fig. 14, is to some extent reminiscent of some species of *Kingena*. In particular, *K. lemaniensis*, which has a proportionately higher median septum than in other species and has a somewhat similar transverse outline of the hood. The small processes or "flaps" to which Smirnova (1960 : 117) refers in her description of the hood of *Belothyris* were compared by her to the lateral "flaps" or flanges seen on the transverse band of *Gemmarcula aurea* Elliott from the Upper Aptian of Faringdon, Berkshire. Processes or flanges similar to those noted by Smirnova have been seen on the lateral extremes of the transverse band or hood of *K. lemaniensis* and *K. convexiformis* from the Shenley Limestone, Leighton Buzzard, Bedfordshire. It is thought, here, however, that these processes are in no way comparable to those of

FIG. 5. Cameralucida drawing of the brachial loop of *Zittelina impressula* (Quenstedt) from the Upper Jurassic, Malm, Germany. B. 45092. ×15 approx.

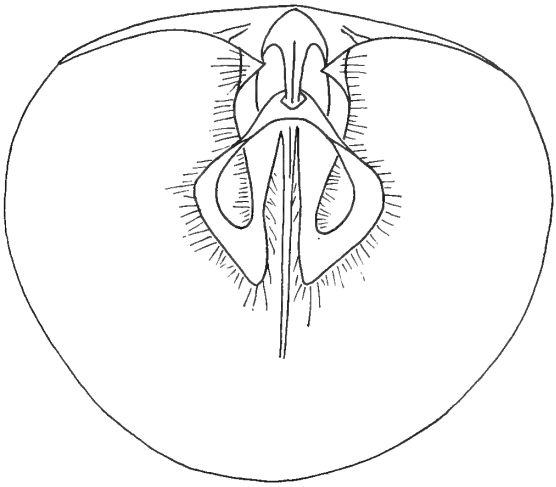


FIG. 6. Cameralucida drawing of the mature brachial loop of *Kingena pentangulata* (Woodward) from the Upper Chalk, *mucronata* Zone, Norwich, Norfolk, showing the length of the septum in proportion to the length of brachial valve. BB. 45789. ×20 approx.

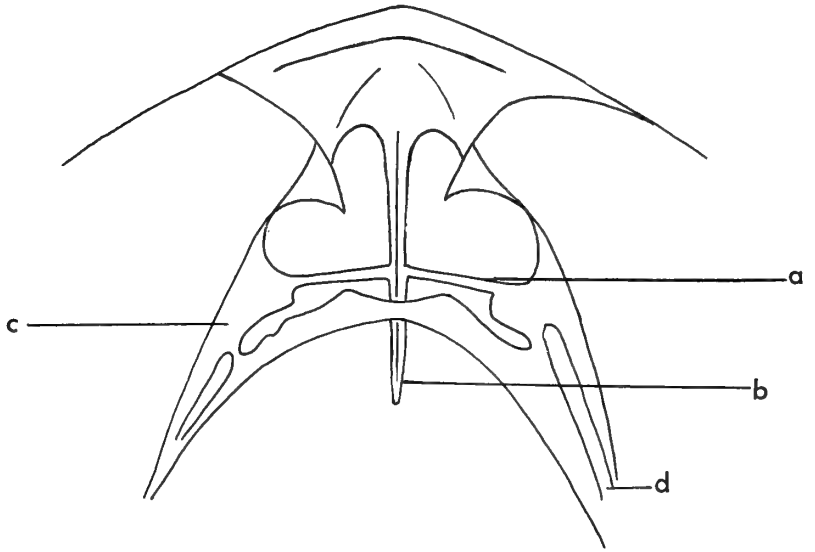


FIG. 7. Drawing of the brachial loop of *Laqueus californicus* from Recent seas off California showing a. connecting bands to septum. b. comparatively long septum. c. laqueiniform loop. d. lateral lacunae in transverse hood. ×3 approx.

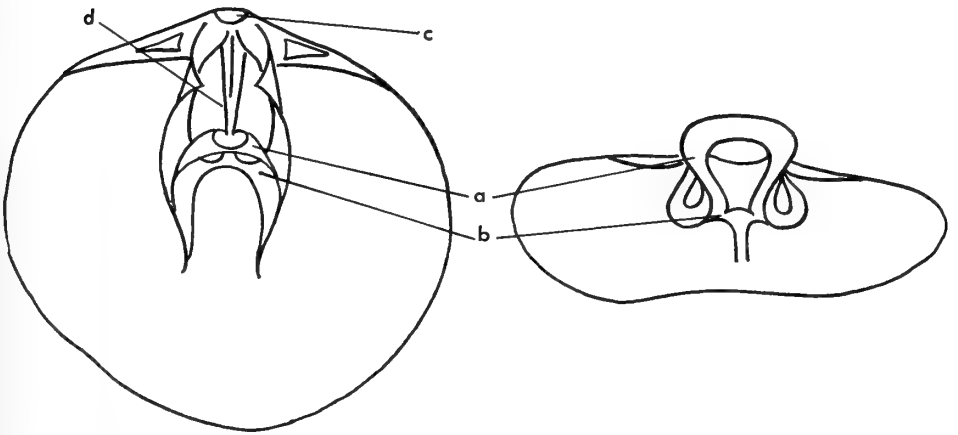


FIG. 8. Drawing of *Frenulina sanguinea* from Recent seas off the Philippines. a. frenuliniform hood. b. descending branches with broad connecting bands to the short septum. c. cardinal process. d. median septum. ×4.

Gemmarcula aurea Elliott. They are smaller in proportion to the rest of the loop and are directed ventrally, whereas, in *Belothyris plana*, these structures are seen to be deflected dorsally.

The brachial loop of *Tulipina* is known only from the serial sections of the type species *Terebratula koutaisensis* (de Loriol) published by Smirnova (1962). It shows the double attachment of the loop branches to median septum but also shows that no hood or expanded transverse band is developed, the ascending branches being attached directly to the septum. The descending branches form an attachment to the septum at a point when they are almost at right-angles to the septum, that is, late in their development.

The short lateral concavo-convex plates at the base of the median septum are unlike any structure so far examined in the Kingeninae. They may have provided additional support to the lophophore.

In *Kingena* and *Zittelina*, as in some genera within the Zeilleriidae, the brachial loop is seen to have numerous small spines attached to the outer surface of the branches. These spines originate at the extreme posterior end of the loop, becoming more elongate anteriorly and at the distal ends of the loop. No such spines occur in the Recent genera *Laqueus* and *Frenulina* but additional spiny outgrowths have been observed on the dorsal surface of the branches in early loops of *Macandrevia cranium*, but these disappear as the loop develops towards maturity.

Definition of relative size in the Kingeninae. For the purpose of this work only, the term LARGE is applied to a specimen with external dimensions of approximately :

15–26 mm long,
10–16 mm wide.

MEDIUM would approximate :

10–14 mm long,
4–9 mm wide.

SMALL would be approximately :

2–9 mm long,
3–8 mm wide.

Variation within these limits occur in some species, but these are always noted in descriptions.

VII. SHELL STRUCTURE

Rapid advances have recently been made in the study and understanding of the shell structure of both articulate and inarticulate brachiopods. Such advances are due largely to the splendid series of papers on this subject by Williams (1956, 1965, 1966, 1968) who has revived the interest sparked off by Carpenter (1843, 1855), King (1867) and Blochmann (1908) and has projected a further dimension into the concept of the phylogeny of the group.

The Cambridge "Stereoscan" electronmicroscope has been used in the present investigation for the purpose of comparing mosaic patterns on the inner surface of the shells of fossil species of *Kingena* with those of some Recent Dallinidae and other Terebratellacean forms.

In general terms, the mosaic pattern in the Kingeninae consists of a fairly even distribution of acute diamond shaped ends to the terminal faces of the secondary shell fibres, not altogether different from any other Terebratellacean brachiopods. Minor differences, however, are present which can only be explained by comparison with Recent forms which are related, either directly to the Dallinidae or diverge to such an extent as to allow a contrast to be drawn.

The general pattern of the shell mosaic in *Kingena* appears to conform to that observed in Recent Dallinidae. The distribution and relative size of the endopunctae, on the other hand, differ considerably. In *K. lemaniensis* shown here, Pl. 12, fig. 3, the endopunctae appear large in comparison to the terminal ends of the fibres, whereas in other Dallinidae of Recent origin, such as *Macandrevia cranium*, Pl. 12 fig. 6, and *Campages basilanica*, Pl. 12, fig. 4, the endopunctae are considerably smaller and more numerous than in *Kingena*. They also appear to be arranged in distinct rows almost equidistant from one another. This arrangement of the endopunctae seems to have more in common with *Terebratella dorsata*, Pl. 12, fig. 2, which has a more numerous distribution of caecae.

By way of contrast, the mosaic pattern of two species of *Laqueus* shown on Pl. 13, figs. 1 & 2, is seen to have a more quadrate outline or less acutely diamond-shaped than in the Kingeninae. Even at points just anterior to the muscle-marks and also at the anterior margin the general outline of the mosaic in *Laqueus* is consistently more quadrate.

VIII. SYSTEMATIC DESCRIPTIONS

Elliott (1948 : 311) erected the subfamily Kingeninae for *Kingena* Davidson, 1852. The extraordinary differences in brachial loop structure, such as, the double attachment of brachial branches to septum and the expanded transverse band or kingeniform hood in the mature Kingeninae which Elliott recognized, are here thought to be sufficiently distinct as to warrant further separation from the main family, Dallinidae. The family Kingenidae Elliott, 1948 is here proposed, nom. transl. for Kingeninae Elliott, 1948.

Superfamily ***TEREBRATELLACEA*** King, 1850
Family ***KINGENIDAE*** Elliott, 1948 nom. transl.
Subfamily ***KINGENINAE*** Elliott, 1948
Genus ***KINGENA*** Davidson, 1852

TYPE-SPECIES. *Terebratula lima* Defrance, 1828

Kingia Schloenbach, 1865
Kingena Stoliczka, 1872
Kingena Dall, 1877
Kingena Hall & Clarke, 1894
Kingena Schuchert, 1897
Kingena Schuchert & LeVene, 1929
Kingena Hertlein & Grant, 1944
Kingena Elliott, 1965

EMENDED DIAGNOSIS. Small to large biconvex, elongate-oval to elongate-pentagonal ; rectimarginate to faintly uniplicate to ligate ; test thin, pustulate. Umbo short, massive to slightly produced, suberect ; foramen subcircular, permesothyridid ; deltidial plates disjunct. Muscle marks and pallial sinuses faint. Cardinal process small, hinge-trough concave, shallow, broad, supported by thin long, moderately high median septum. Loop with modified transverse band, or funnel-shaped hood doubly attached to septum, developed from early precampagiform and campagiform stages.

EMENDED DESCRIPTION. The genus comprises a group of variable but distinct biconvex, pentagonal Terebratellacean brachiopods, ranging in length from less than five millimetres to over twenty-six millimetres, and in width from three to approximately eighteen millimetres. They can be distinguished from all other Terebratellacean brachiopods by the pustulate or spinulose ornament covering both valves.

Internal characters. The umbonal cavity of the pedicle valve is infilled with callus, uniting the dental lamellae and afixing them to the floor of the valve.

Although past descriptions have always included the presence of a cardinal process, this character is particularly poorly developed and is rarely seen in transverse serial sections. It is composed of a flattened concave disc situated at the extreme posterior end of the brachial valve.

The dorsal surface of the brachial loop is covered with short spines which project into the brachial cavity and may have been used as additional support for the lophophore.

The descending branches originate from the distal end of the hinge-trough and curve in towards the septum, extending a short, broad band of connection, fusing with the septum and connecting with the extended ends of the broad, conical transverse band or kingeniform hood of the ascending branches above it.

The median septum in the brachial valve is long, extending to over two-thirds the length of the valve.

The genus has an estimated geological range of Lower Albian to Lower Maastrichtian.

Kingena lemaniensis (Pictet & Roux)

(Pl. 1, figs. 1–4)

1847 *Terebratula lemaniensis* Pictet & Roux : 538, pl. 51, figs. 5–7.
1863 (*Terebratula*) *Megerlia lima* Davidson ; Ooster : 35, pl. 12, fig. 16.
1900 *Terebratula lemaniensis* Pictet & Roux ; Ficheur : 573.
1903 *Kingena newtoni* Walker : 259, pl. 18, figs. 5, 7.

EMENDED DIAGNOSIS. Elongate-oval to elongate-pentagonal *Kingena* with a distinct terebratulid aspect. Rectimarginate to markedly uniplicate. Unbo suberect, short, massive. Beak-ridges distinct ; interarea extensive, deltidial plates well exposed. Foramen large, circular.

LECTOTYPE. CB. 2530 here selected from fifty-two specimens in the Pictet Collection at the Musée d'Histoire Naturelles, Geneva, Switzerland. It is figured here, Pl. 1, figs. 1a–c.

HORIZON AND LOCALITY. Lower Albian, Grand Bornand, France.

DESCRIPTION. The largest species of *Kingena* so far recorded from any locality. It maintains an average length of approximately 25 mm., width of 20 mm., and thickness of 16 mm.

As in all other species of *Kingena*, the early stages of growth in *K. lemaniensis* are almost circular in outline becoming progressively elongate in intermediate and adult stages.

Decidedly terebratulid in general outline, it develops a well marked uniplication of the anterior commissure due to lateral constriction of the anterior part of the shell in the later stages of growth. There is a fair degree of marginal thickening in the gerontic stages.

The umbo, though massive, is slightly produced and the extensive interarea well exposed. The permesothyridid beak-ridges which border the interarea are sharply defined.

Although the shell surface is covered with the characteristic pustules or granules, they are seen on the typical form from French and Swiss localities only when enough shell has been preserved. This is a rare occurrence, but when seen, they appear as small or fine rounded pustules, evenly distributed over the shell surface. This type of pustulation is more often seen on the shells of the British equivalent of the species at Leighton Buzzard, Bedfordshire. Here, however the pustules are not as well marked on mature individuals as on the shells of young forms.

Internal characters. Essentially the same as for the genus but, from an examination of a reconstruction made of the brachial loop from transverse serial sections, it is possible to determine certain minor variations from the typical loop structure of Upper Chalk species. These are seen as a less developed kingeniform hood and a more brief attachment of descending branches to septal pillar. The serial sections have been compared with those of *Kingena pentangulata* (Woodward) from the Upper Senonian of Norfolk and figured here, Fig. 13.

REMARKS. *Kingena lemaniensis* is a notable brachiopod species in a typical faunal assemblage which characterizes the Lower Albian deposits of Mont Saxonet, Perte du Rhône, Goudiniere and Reposoir in the Haute Savoie, France. Specimens from these localities are usually found as dark-brown or black phosphatic internal moulds, although a few specimens have been found with quite well preserved shells.

The species occurs in Britain and was described as *Kingena newtoni* by Walker (1903 : 258) from the Lower Albian, Shenley Limestone of Leighton Buzzard, Bedfordshire. Here it is found in association with a fauna of Terebratulidae and Rhynchonellidae in every respect comparable to that found at the type locality in France. A prominent associated species is *Cyclothyris antidichotoma* (Buvignier) which was recently re-described by Owen (1962 ; 47) from the " Gault " of the Ardennes, who drew attention to the similarity between specimens described and figured by Pictet (1872 : 41, pl. 199, figs. 13–17) and those described from Leighton Buzzard. *Burrihynchia leightonensis* (Walker) and *Cyclothyris mirabilis* (Walker) are also found in association with *K. lemaniensis*. Ficheur (1900 : 573) recorded *K. lemaniensis* in association with " *Rhynchonella* " cf. *antidichotoma* (Buvignier)

from the Lower Albian of Algeria. Ooster, (1863) refers to *Terebratula lemaniensis* specimens in the Berne Museum, Switzerland, which show radiating striae on the shell surface, a feature also noted on well preserved specimens from the British locality.

A species which was described by Walker (1903) as *Zeilleria convexiformis* and which is a common fossil in the Shenley Limestone at Leighton Buzzard, may be related to *K. lemaniensis* but appears to be more elongate with a shorter, truncated umbo and steeper flanks than *K. lemaniensis*. The anterior commissure is rectimarginate to very faintly uniplicate. It is referred here to *Kingena* and is figured Pl. 1, figs. 5 & 6.

MATERIAL. Numerous specimens in the Walker Collection, British Museum (Natural History) of both *K. lemaniensis* and *K. convexiformis*. At least fifty specimens in the collections of the Musée d'Histoire Naturelles, Geneva.

RANGE. Lower Albian.

Kingena spinulosa (Davidson & Morris)

(Pl. 2, figs. 1–6, Pl. 3, figs. 1–7, Text-fig. 9)

1847 *Terebratula spinulosa* Davidson & Morris : 253, pl. 18, figs. 6a-c.
1852 *Kingena lima* Defrance ; Davidson : 42, pl. 4, figs. 24 a-d.
1868 *Kingena lima* Defrance ; de Rance : 163.
1869 *Kingena lima* (Defrance) ; Wiltshire : 185.
1874 *Kingena lima* Defrance ; Price : 353.
1900 *Kingena lima* Defrance ; Jukes-Browne : 79.
1961 *Kingena* sp. ; Peake & Hancock : 303.

EMENDED DIAGNOSIS. Elongate-pentagonal to elongate-oval *Kingena*, approximately 15 mm. long, 14 mm. wide and 9 mm. thick. Rectimarginate to incipiently uniplicate. Umbo suberect, short, massive, truncated by large permesothyidid foramen. Beak-ridges sharp. Deltidial plates, disjunct, well exposed. Interarea extensive. Shell surface covered with large and small pustules or granules. Kingeniform loop supported by long median septum.

HOLOTYPE. B.5260 in the Davidson Collection, British Museum (Natural History) and housed with three other specimens of the same species in a small box. On the back of the box, in Davidson's handwriting, are the words " *Kingena lima* Defr., Gault, Folkestone. The largest of these specimens is the original figured and described by myself in the Annals & Mag. Nat. Hist. pl. XVIII, 1847. "

DESCRIPTION. In the early stages of growth, the species is almost completely circular in general outline, but with anterior growth, becomes pentagonal to elongate-oval in outline in the later stages.

The lateral profile varies from plano-convex to biconvex. The characteristic ornament of pustules or spinose granules occurs in this species as a mixture of both large and small granules, almost conical in shape, and distributed evenly but more sparsely over the shell surface than in other species. Enlarged photographs of the shell ornament in *K. spinulosa* are shown on Pl. 13, figs. 3, 4 for comparison with similar ornament on the surface of *K. lima* (Defrance), the type species from the Upper

Chalk of Margate, Kent. Davidson's enlarged drawings of the shell surface of his specimen (pl. 4, fig. 24d) is somewhat misleading, as it shows the tops of the pustule with indentations or depressions which might infer that he thought them to be hollow, as is the case with true spinose ornament. In fact, as has been discussed earlier, these pustules or granular outgrowths are formed from the primary layer of the shell and are completely solid.

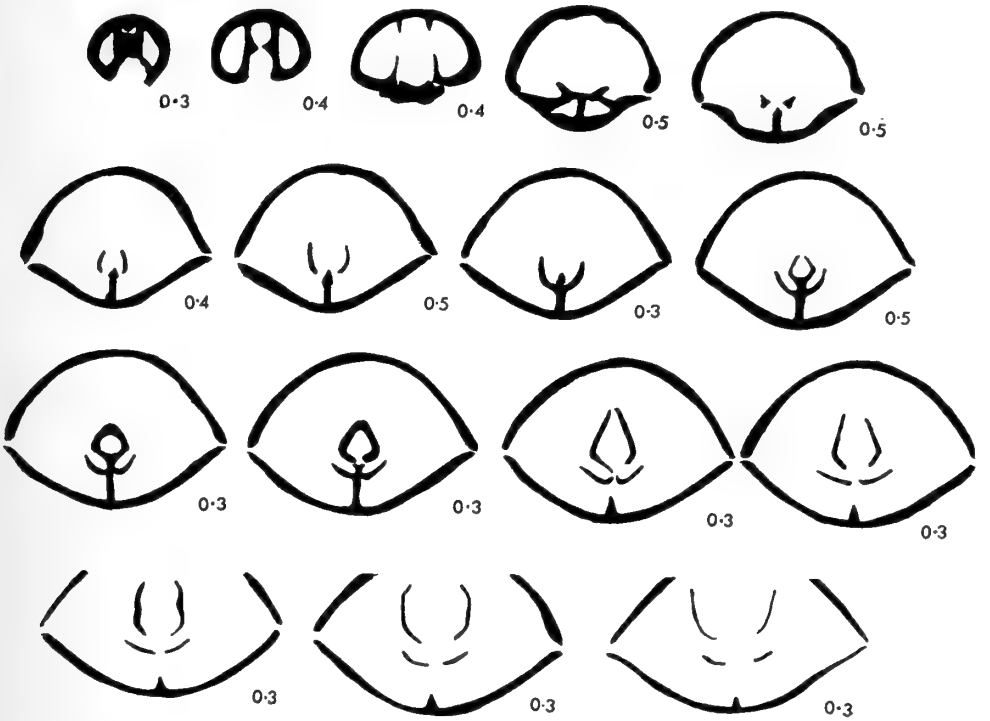


FIG. 9. Sixteen transverse serial sections through *Kingena spinulosa* (Davidson & Morris) from the Upper Albian, Red Chalk, Hunstanton, Norfolk. BB. 45790. ×2.

A common feature in well preserved specimens of *Kingena* from Albian localities is a faint ornament of radiating striae which appears just below the surface of the shell. The pustulose ornament gives the appearance of following the line of striation, but this is purely an illusion. The same effect is noted on specimens where the concentric growth-lines are prominent, the pustules then assuming a semicircular or concentric pattern.

Internal characters. As for the genus.

REMARKS. *Kingena spinulosa* is known only from English Upper Albian localities. Although described by some authors as being fairly common in the Gault, it is no longer easily obtainable from the type locality at Folkestone. De Rance (1868 : 168) in a description of the section at Copt Point, designated this species, under the

name of *Kingena lima* Defrance, one of the main zone fossils of his Bed II. Price (1874 : 353) in a revision of De Rance's section, went even further stating "From the frequency of occurrence of *K. lima* in the zone, I am adopting the conclusion arrived at by Mr. De Rance and propose the name of the bed, the Zone of *Kingena lima.*" He was, of course, describing his Bed X of the Gault at Folkestone.

Kingena spinulosa also occurs as a derived fossil in the Cambridge Greensand, but here it appears as an internal mould and is proportionately smaller than the typical form. Nevertheless, the basic diagnostic features of the species are present in well preserved specimens. It is possible to discern the very faint muscle marks at the extreme posterior end of the brachial and pedicle valves of these moulds. In the brachial valve, they are seen as small triangular areas raised slightly above the surface of the surrounding mould and are shown reproduced here, Fig. 4, p. 45. In the pedicle valve, the marks are less distinct and appear as elongate, broadly triangular strips. It is also noted from these moulds that the septum is proportionately longer in the young specimens.

In the Upper Albian, Red Chalk, at Hunstanton, Norfolk, the species is also recognized. Numerous specimens have been collected from these beds over the past twenty or thirty years by Mr. H. Le Strange. From the specimens collected, are well known marked variants which appear to be less elongate than those found among the typical form. They tend towards greater width, less produced or truncated umbo and some exhibit a faint sulcation of the anterior part of the brachial valve. The early stages throughout the full range of variation, however, agree in every detail with those found in the Gault at Folkestone and from the derived fossils in the Cambridge Greensand.

Although the geographical distribution of this species probably extends as far as the French Upper Albian, no records from continental localities can be found in the literature.

Muir-Wood (1930 : 34) described and figured a specimen under the name of *Kingena spinulosa* (Davidson & Morris) from the Gault of the Samana Range, India. The very poor internal moulds with which she illustrated the species are considered here to be in no way comparable to those of *Kingena spinulosa* as originally defined by Davidson and Morris (1847 : 253, pl. 18, figs. 6, a-c). This form has, therefore, been renamed here in honour of the late Dr. H. M. Muir-Wood as *Kingena muirwoodae* nom. nov. pro. *Kingena spinulosa* (Davidson & Morris) ; Muir-Wood (1930 : 34, pl. 5, fig. 6) non *Kingena spinulosa* (Davidson & Morris) 1847.

RANGE. Upper Albian.

DIMENSIONS OF TOPOTYPE AND OTHER SPECIMENS.

	Length	Breadth	Thickness
BB. 3296	16 mm	14 mm	10.5 mm
BB. 3297	12 mm	10 mm	7.7 mm
BB. 4628	11.5 mm	10 mm	7 mm
BB. 4629	9.8 mm	10 mm	6 mm

All the above specimens are in the British Museum (Nat. Hist.) and were collected from the Gault at Folkestone.

The following specimens are in the Sedgwick Museum, Cambridge, and are from the Upper Albian, Hunstanton.

	Length	Breadth	Thickness
B. 41751	16.5 mm	15 mm	10 mm
B. 41739	16 mm	16 mm	9 mm
B. 41762	14 mm	14 mm	8 mm

Kingena arenosa (d'Archaic)

(Pl. 4, figs. 1–7, Pl. 5, figs. 1–5. Text-fig. 10)

1846 *Terebratula arenosa* d'Archaic : 324, pl. 21, figs. 1a-e, 2a, 3a, b.
1847 *Terebratula lima* d'Orbigny ; d'Orbigny : 98, pl. 512, figs. 1–5.
1852 *Kingena lima* Defrance ; Davidson, pl. 4, figs. 21, 22, 25.
1903 *Kingena lima* Defrance ; Jukes-Browne & Hill : 113, 248, 257.

EMENDED DIAGNOSIS. Medium to large *Kingena*. Broad, oval-pentagonal, width almost equal to length. Short, massive, suberect umbo truncated by large, circular foramen. Well defined, extensive interarea bordered by sharp beak-ridges. Deltidial plates disjunct, well exposed. Rectimarginate to sulcate to faintly uniplicate anterior commissure. Growth-marks distinct. Pustulation fine, evenly distributed.

NEOTYPE. The d'Archaic Collection was composed largely of material borrowed from other collectors. The whereabouts of the brachiopods used to illustrate his monograph (1846) is unknown and most of the specimens are thought to have been lost. No trace of the specimens described as *Terebratula arenosa* and figured on his pl. 21 can be found in France or Belgium and it is therefore considered necessary to propose a neotype for this species in order that it should once again become established in the literature.

The specimen here proposed as neotype is from the Tourtia of Tournai, Belgium and is in the collections of the Institut royal des Sciences naturelles de Belgique, Brussels no. I.G. 8261. It is figured here, pl. 4, fig. 3a-c.

DESCRIPTION. Perhaps one of the most variable of any of the species of *Kingena*, the typical form, as defined here, is nonetheless distinctive, being fairly large, flattened form in maturity, with well marked sulcus on the anterior part of the pedicle valve. When further developed in gerontic specimens, this sulcus gives rise to a faint uniplication of the anterior commissure. Well developed, almost step-like growth-lines are common features on well preserved specimens.

Unlike the ornament of *Kingena spinulosa* from the Upper Albian, the pustulation on the shell surface of *K. arenosa* is of uniform size, being fairly fine and evenly distributed over the surface of the valves.

A broad hinge-line in the typical form gives rise to an extensive interarea bounded by sharp beak-ridges. The large, circular foramen truncates a short, massive umbo. The anterior profile is elliptical.

In early growth-stages the species is plano-convex to just biconvex, becoming acutely biconvex with, sometimes, marked inflation of the brachial umbo, which diminishes with lateral and anterior growth of the shell. The pedicle valve maintains its early acute convexity throughout all growth stages.

Internal characters. As for the genus. See Fig. 12, p. 61.

Remarks. Most of the specimens examined from the type locality are in museum collections. In the main, this material has been collected from two or three sites within the type area of Gussignies near Tournai, Belgium. The deposits at these localities, known as the Tourtia, are generally thought to be of condensed Upper Albian and Cenomanian age. Apart from the presence of *Terebratula capillata* d'Archaic, which is known only from Albian localities in Britain, the brachiopod fauna in the Tourtia of Belgium contains very little of Albian significance. However, until more faunal evidence is available, the exact age of the deposits remains indefinite.

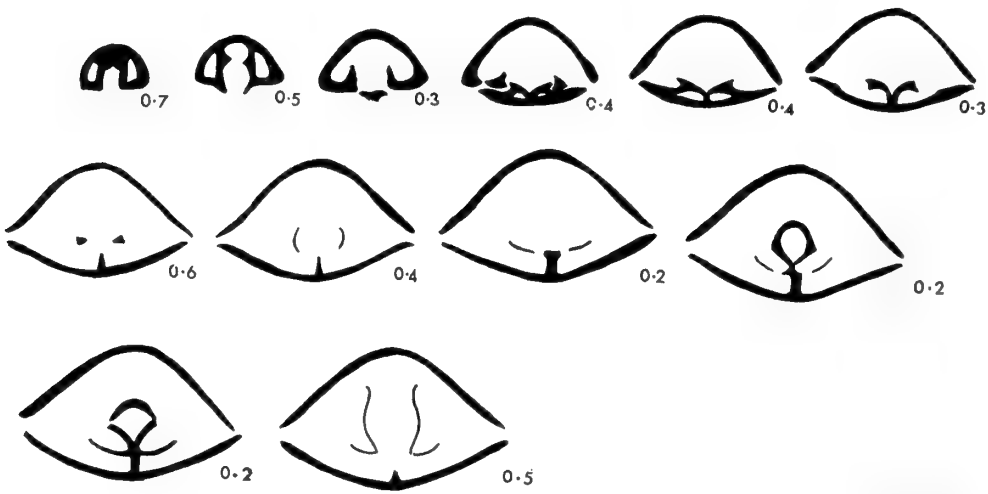


Fig. 10. Twelve transverse serial sections through *Kingena arenosa* (d'Archiac) from the Tourtia of Tournai, Belgium. BB. 45784. ×2.

In the same way, the " Greensand " deposits at Warminster, Wiltshire, are of indefinite age, no correlation with coastal sections having been made so far. Here again, the beds yield what is considered to be a typical Cenomanian brachiopod fauna and *Kingena arenosa* (d'Archaic) occurs in these beds with *Cyclothyris difformis* (Val. in Lamarck), " *Terebratula* " *ovata* (J. de C. Sowerby), *Dereta pectita* (J. Sowerby and *Orbirhynchia mantelliana* (J. de C. Sowerby). The Warminster beds are no longer exposed.

In Britain, *K. arenosa* occurs in the sandy facies of the Middle Cenomanian at Wilmington, Devonshire, in the Cenomanian Beds B, at Bovey Lane sandpit and from beds of equivalent age in the coastal sections from Branscombe, Hooken, Seaton, south Devon and along the Dorset coast to Lulworth. It is also found in the middle Cenomanian deposits at Culver and Compton Bay, Isle of Wight.

Similarly, in France, *Kingena arenosa* occurs in the Lower and Middle Cenomanian Limestone at Bléville, and at Cap le Heve near Le Hâvre, Normandy.

At Essen in North Germany, the species occurs in the Lower Cenomanian deposits

known as the " Essen Tourtia " or " Essen Greensand " and may be the same species described as *Terebratula pectoralis* by Roemer (1840 : 42) and figured (pl. 7, fig. 19a-c), but the illustration is poor and the whereabouts of the specimen unknown and it is here regarded as *nomen. dubium.* Reuss (1845) described a specimen under the name *Terebratula pectoralis* Roemer and figured a specimen (pl. 26, fig. 12) from the Plänerkalk of Kutschlin, Czechoslovakia. This may belong to the species *K. arenosa* (d'Archaic) although the specimen figured is lacking in some of the more diagnostic features, such as, pustulation of the shell and no median septum is visible from the figure.

Apart from the type locality at Tournai, the species also occurs at Montignies-sur-Roc and Chercq (Pont-à-Rieu) in Belgium.

K. arenosa differs from *K. spinulosa* from the Upper Albian in its regular or uniform size of pustules on the surface of the shell and in its different dimensions. It is proportionately wider than any species of *Kingena* described here and the umbonal characters are dominated by a large foramen.

DIMENSIONS OF NEOTYPE AND OTHER SPECIMENS

	Length	Breadth	Thickness
I.G. 8261 Neotype	16 mm	16 mm	11.9 mm

ADDITIONAL MATERIAL

B.M. = British Mus. (Nat. Hist.)
I.G. = Inst. roy. Sci. Brussels

	Length	Breadth	Thickness
B.M. 88760 Warminster	28 mm	29 mm	19.9 mm
B.M. B.35456, Montignies-sur-Roc.	14 mm	13.6 mm	11.5 mm
I.G. Unregd. Duplicate, Bléville, France.	14 mm	14 mm	10 mm

FURTHER MATERIAL USED. B.M. B. 82713–17, Warminster. B.M. B.491 Warminster. B.M. B. 8268–70, Warminster. B.M. BB. 9319, Lulworth Cove, Dorset. B.M. BB. 7053–56, Bindon Steps-slips, Seaton, Devon. B.M. BB. 42412, Cran d'Escalles, nr. Cap Blanc Nez. B.M. B. 35197, Le Hâvre, Normandy. B.M. B. 15474, Essen, Germany. B.M. B. 35692, Essen, Germany. B.M. B. 85103–6, Montignies-sur-Roc, Belgium. B.M. B. 35456, Montignies-sur-Roc, Belgium. I.G. 5096, Tournia. I.G. 12515, Chercq (Pont-à-Rieu), Belgium.

Kingena concinna sp. nov.

(Pl. 5, figs. 6, 7, 8. Pl. 6, figs. 4–6, Text-fig. 11)

1852 *Kingena lima* Defrance ; Davidson : 44, pl. 5, figs. 1, 2, 4.
1903 *Kingena lima* Defrance ; Jukes-Browne : 43, 192, 204, 224.

DIAGNOSIS. Shell oval, acutely biconvex. Umbo massive, incurved ; foramen small. Anterior commissure rectimarginate to just ligate. Finely pustulate Hingeline narrow, beak-ridges short, indistinct.

HOLOTYPE. BB. 93758 in the British Museum (Natural History), collected from the Middle Cenomanian, *rhotomagense* zone, (Bed 5 of Price), Foreshore between Folkestone and Dover, Kent.

DIMENSIONS OF HOLOTYPE. 15 mm. long, 13 mm. wide and 10 mm. in thickness.

DESCRIPTION. A small globose *Kingena* with a distinctly terebratulid aspect. The general outline is unmistakably oval but some variants have a tendency to straighter or subparallel sides and foreshortened anterior. This variant is more commonly found in assemblages from the Cambridge Greensand, although it does occur at Folkestone and Dover. The rounded umbo is slightly incurved, obscuring the deltidial plates. The lateral profile shows the acute binconvexity of the shell and a degree of posterior inflation of the brachial umbo.

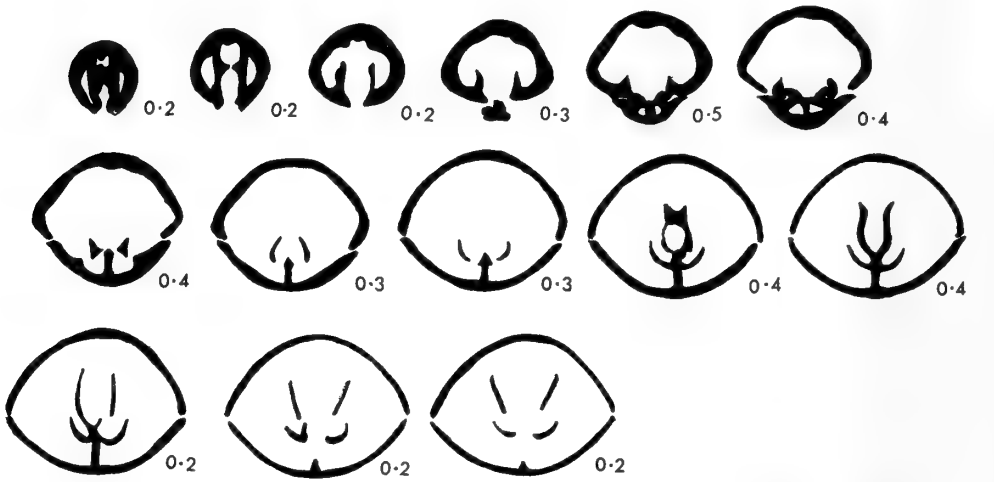


FIG. 11. Fourteen transverse serial sections through a specimen of *Kingena concinna* sp. nov. from the Middle Cenomanian, *rhotomagense* Zone of Folkestone, Kent. BB. 45785. ×3.

REMARKS. This small species has often been misidentified as *Terebratula squamosa* Mantell and occurs with this species at Dover and Folkestone.

It is thought that *K. concinna* occurs in the Totternhoe Stone and possibly in the basal beds of the Plenus Marls, but specimens collected from these beds are often damaged or crushed. In Lincolnshire it occurs in the *H. subglobosus* zone (Yorkshire equivalent) at Louth and has been collected from a similar horizon at Kiplingcotes Valley, East Yorkshire by Mr. C. W. Wright.

The species can be distinguished from other described species of *Kingena* in its extreme convexity or semiglobose outline and general terebratulid appearance.

PARATYPES. All from the collections in the British Museum (Natural History). B. 25030, Burwell, Cambridge. B. 51479, West Cliffs, Dover. BB. 7446, Tinhead, near Bratton, Wiltshire. B. 55092 Pit 2, near waterworks, Hubbard's Valley, Louth, Lincolnshire. BB. 45811, Rifle Butts Pit, Kiplingcotes Valley, E. Yorkshire.

Kingena elegans sp. nov.

(Pl 6, figs. 1–3)

1968 *Terebratula* (*Megerleia*) *lima* Defrance ; Schloenbach ; 32, pl. 3, figs. 1, 2.
1904 *Kingena lima* Defrance ; Jukes-Browne : 289, 229.
1942 *Kingena lima* (Defrance) ; C. W. & E. V. Wright : 117.

Diagnosis. Small to medium *Kingena* ; elongate-pentagonal. Umbo slightly produced. Hinge-line broad, interarea extensive. Foramen large, beak-ridges sharp, permesothyridid. Anterior commissure sulcate.

Holotype. B. 55241 in the British Museum (Natural History), from the Turonian, *Holaster planus* Zone, Pit 8, Boswell Farm, $3\frac{1}{2}$ miles north west of Louth, Lincolnshire.

Description. A trim, neat-looking, regular pentagonal shell with well marked growth-lines. The average length is 14 mm., width 11 mm., and thickness 9 mm. The umbo is characteristic of the species being dome-like, suberect and with wide interarea and well marked beak-ridges. There is an even degree of convexity of each valve with a shallow sulcation of the anterior part of the brachial valve. A corresponding flattening of the pedicle valve in the anterior region is bordered by faint, slightly radiating, carinae, one on either side of the flattened area.

Internal characters. As for the genus.

Remarks. *Kingena elegans* was originally described as *Terebratula* (*Megerleia*) *lima* from the Turonian, Galeriten-Schichten of north Germany by Schloenbach (1868). It is the least variable of all species of *Kingena* and maintains its characteristic elongate-pentagonal outline throughout the full range of its geographical distribution.

In England the species occurs chiefly in the *Holaster planus* zone at Kiplingcotes, Yorkshire and at the same horizon from Louth, Lincolnshire, but specimens have been collected from the *Terebratulina lata* Zone of Swaffham, Norfolk. A single specimen, somewhat larger than the typical, has been collected by Mr. Christopher Wood, Institute of Geological Sciences, from the Turonian, *H. planus* Zone of Reed Quarry, near Royston, Hertfordshire, and probably marks the approximate southern limits of the species in this country.

Kingena elegans differs from *K. pentangulata* (Woodward) in its proportionately smaller dimensions, regular pentagonal outline, marked growth-lines and anterior sulcation of the brachial valve.

Specimens collected from Yorkshire and Lincolnshire are often pink in colour. This colouration of the shell is not an uncommon feature among specimens collected from other horizons within the Middle and Upper Chalk. It is probably the remains of natural pigment of the shell, a common enough character in some of the Recent terebratellacean brachiopods. It is also noted on specimens of *Kingena mesembrina* (Etheridge) from the Gingin Chalk of Western Australia and Elliott (1952 : 5) drew attention to this in his description of the species.

Range. The species appears to be confined to the Turonian.

Dimensions of holotype. 11·5 mm. long, 10 mm. wide, 7 mm. thick.

PARATYPES. All in the British Museum (Natural History). B. 55242–45, Boswell Farm, near Louth. (Probably *T. lata* zone). B. 55222–26, Wyham House, 6 miles N.N.W. of Louth. B. 93438–46, No. 23a. Swaffham Cutting, Norfolk. (*T. lata* zone).

Kingena mesembrina (Etheridge)

(Pl. 6, fig. 9 a-c)

1913 *Magas mesembrinus* Etheridge *fil.* : 15, pl. 2, fig. 5–8.
1952 *Kingena mesembrina* (Etheridge) ; Elliott : 4, pl. 1, figs. 1–13.

As this species has been reviewed as recently as 1952 and has been adequately described by Dr. G. F. Elliott, it is not considered necessary to re-describe it in detail for the purpose of the present work. Elliott's diagnosis and a shortened version of his excellent description are given below. A duplicate specimen obtained from the Gingin Chalk and kindly presented to the British Museum (Natural History) by Dr. Pat Coleman of the Geological Department, University of Western Australia, is figured here, Pl. 6, fig. 8a-c. This specimen compares favourably with the photograph of the original type specimen which Etheridge figured (1913 : pl. 2, figs. 5, 6).

DIAGNOSIS. Shell about 18 mm. long, 16 mm. wide and 9 mm. thick, biconvex rounded pentagonal to elongate-oval, test thin, externally finely granulose and conspicuously punctuate, anterior commissure feebly sulcate. Umbo short suberect, truncated ; foramen moderately large, circular, permesothyrid ; deltidal plates disjunct and obscured by the beak-ridges, hinge-line terebratulid. Hinge-teeth supported by dental lamellae, joined by sessile pedicle-collar. Cardinalia showing strong fused inner socket-ridges and crural bases, wide hinge-trough and transverse cardinal process ; kingeniform loop supported by a short median septum. Muscle marks and pallial sinuses faint.

NEOTYPE. The original specimen figured by Etheridge (1913) is mislaid or lost and the whereabouts of any paratypic material unknown. A specimen figured by Elliott (1952) is here proposed as neotype in place of the specimen which Etheridge figured (pl. 2, fig. 5–8). Elliott's specimen is one of twenty-one hypotypes in the collections of the Department of Geology, University of Western Australia and is the specimen figured by him (1952 : pl. 1, figs. 12, 13).

DESCRIPTION. This shell varies somewhat in outline, though easily recognizable. Specimens which are rounded pentagonal in outline include the largest individuals. The test for the species as a whole shows on well-preserved specimens the fine external surface granules characteristic of the genus ; the punctation is coarse and close-set.

REMARKS. The species described by Elliott seems to have a shorter septum than in some of the European forms of equivalent age, but the rest of the internal characters appear to be comparable.

Kingena lima (Defrance)

(Pl. 6, figs. 7–8, Pl. 7, fig. 4a-c, 5a-c, Text-fig. 12)

1828 *Terebratula lima* Defrance : 156.
1863 *Terebratula* (*Kingena*) *sexradiata* (J. de C. Sowerby) ; Deslongchamps : 292, pl. 7, fig. 5–8.
1900 *Kingena lima* Defrance ; Rowe : 300, 363.
1904 *Kingena lima* Defrance ; Jukes-Browne : 42, 80, 221.
1908 *Kingena lima* Defrance ; Rowe : 338.

Diagnosis. Small rounded-pentagonal *Kingena* ; plano-convex to biconvex rectimarginate. Umbo massive, suberect ; beak-ridges distinct. Foramen large circular, permesothyridid. Growth-lines numerous, distinct. Pustulation uniform evenly distributed.

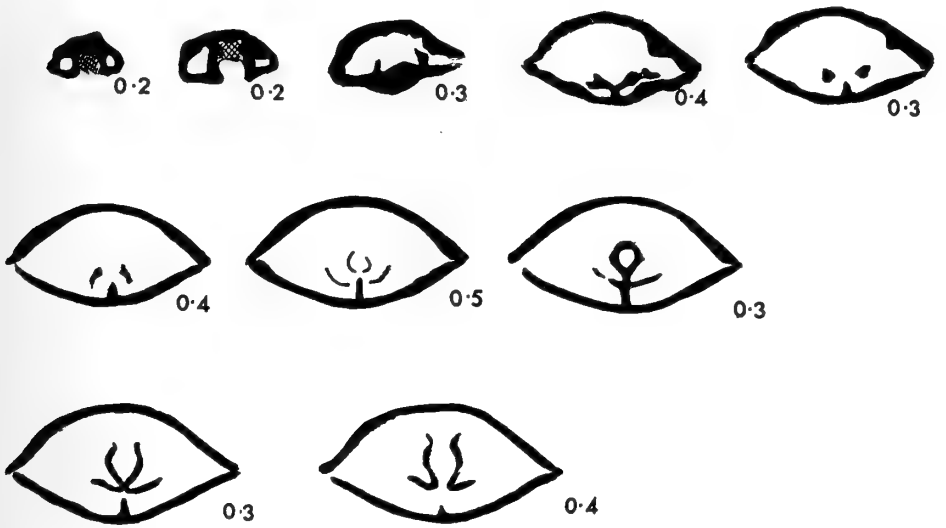


Fig. 12. Ten transverse serial sections through a specimen of *Kingena lima* (Defrance) from the Upper Chalk, *marsupites* Zone, Margate, Kent. BB. 45786. ×3.

Neotype. There is very little evidence of a type specimen or specimens having been used by Defrance in his original description of the species in 1828. It is more likely that, following the practice of palaeontologists of the time, he established the species on knowledge obtained from several examples of what he considered to be a typical or characteristic fossil of the Chalk. His locality details were vague and he quotes " collected from the Chalk in the district of Beauvais " and the stratigraphical details are for pure speculation.

Since there can be no certainty of either the morphological details or the stratigraphical age of the species described by Defrance and, since the Defrance Collection was, in any case, destroyed by the allies during the second World War, a neotype for *Kingena lima* (Defrance) is proposed here.

Difficulty in obtaining suitable material from any French localities within the

Beauvais district or any comparable site, has led me to select a specimen from the Upper Chalk of *Marsupites testudinarius* Zone from Foreness Point, Margate, Kent and is in the collections of the British Museum (Natural History) no. B. 79709. It is figured here, Pl. 7, figs. 4a-c.

DIMENSIONS OF NEOTYPE. 12 mm. long, 11.4 mm. wide and 6 mm. thick.

DESCRIPTION. The length and breadth of this species are almost equal, but variation extends to more elongate or elongate-oval and more robust or more acute convexity. A very strong feature of the umbo is the proportionately large foramen, sharp beak-ridges and marked extensive interarea exposing the conjunct deltidial plates.

The anterior commissure remains rectimarginate but a faint sulcus is developed in the margin of the more elongate variants or older individuals.

K. lima can be distinguished from all other species of *Kingena* by its very characteristic rounded-pentagonal outline, plano-convex profile and marked umbonal features. It is one of the smallest species described.

Because of the comparative rarity of occurrence of this species, records of distribution and horizontal range have been obtained largely from collected material found in museum collections. It appears, however, to range from the *Micraster cortestudinarium* zone of the Lower Senonian to the *Marsupites testudinarius* zone of the Middle Senonian. It is more commonly found in the *Uintacrinus socialis* and *Marsupites* bands in the Senonian at Margate and St. Margaret's Bay, Kent. It is also fairly common at equivalent horizons in the Chalk of Angmering and Burpham in Sussex. A few specimens, although somewhat fragmentary, have been obtained from these bands at Flamborough Head, Yorkshire.

MATERIAL. *M. cortestudinarium* Zone. B. 79797–8, Dover, Kent. B. 93483, Swaffham, Norfolk.

M. coranguinum Zone. B. 79691–705, Thanet Coast. B. 79706, St. Margaret's Bay, Kent.

Uintacrinus socialis Zone. B. 97084, Devizes Rd., W. of Salisbury. B. 79710–23, Thanet Coast. B. 91929–41, Highfield, W. of Salisbury.

Marsupites testudinarius Zone. B. 92049, Bishop Down, nr. Salisbury. B. 47968, Pit. 29, Highdown Hill, E. of Angmering, Sussex. B. 47974, Pit. 27, Burpham river cliff, S. of St. Mary's Church, Burpham, Sussex. B. 96216–7 Foreness Point, Margate. Kent.

All the above specimens are in the collections at the British Museum (Natural History).

Kingena sexradiata (J. de C. Sowerby)

1850 *Terebratula sexradiata* J de C. Sowerby *in* Dixon : 346, 354, pl. 27, fig. 10.
1852 *Kingena lima* (Defrance) ; Davidson : 42.

EMENDED DESCRIPTION. Small *Kingena* measuring 8·9 mm. in length and 8·5 mm. in width. The measurement of the thickness cannot be estimated owing to the nature of the preservation of the specimen. The specimen is slightly crushed and

completely surrounded by the chalk matrix on the ventral side. It is possible to discern a faint, shallow sulcus on the brachial valve which originates from the umbonal area and broadens gently anteriorly. This sulcus is bordered by faint carinae, one on either side. The very faint radiating striae which Sowerby observed are just visible, but appear to number more than six. The median septum is clearly visible and extends to over two-thirds the length of the brachial valve. The shell surface is finely pustulate, the pustules being of even size and distribution. A faint pink colouration of the shell is noticeable.

HOLOTYPE. In the British Museum (Natural History), no. 30584, from the Chalk of Sussex.

REMARKS. This is a very doubtful species since it is not known from exactly what horizon the original specimen was collected. The type specimen is the only specimen known to exist.

Kingena blackmorei sp. nov.

(Pl. 7, figs. 1–3, Pl. 8, fig. 1)

1904 *Kingena lima* Defrance ; Jukes-Browne ; 66, 85.
1964 *Kingena pentangulata* (Woodward) ; Muir-Wood : 148, pl. 52, fig. 6.

DIAGNOSIS. *Kingena*, broadly pentagonal, width often equal to length. Plano-convex to biconvex. Rectimarginate to incipiently uniplicate. Hinge-line broad ; interarea extensive, deltidial plates well exposed. Umbo short, massive, truncated. Foramen large, subcircular. Median septum long. Pustulate ornament fine, evenly distributed. Growth marks numerous, indistinct.

HOLOTYPE. B. 92779 in British Museum (Natural History), collected from the Upper Senonian, *Gonioteuthis quadrata* Zone, East Harnham, Wiltshire and figured here, Pl. 7, fig. 2.

DESCRIPTION. A large *Kingena* with an average length of 18 mm., width 17·6 mm. and thickness 10·4 mm. Although characteristically subcircular in early growth-stages, it remains constantly pentagonal through later stage of growth and in gerontic development. The brachial valve remains flattened in all stages, developing a very slight convexity in the umbonal region in early growth and maintaining a slight inflation of this part of the valve in later stages. The length of the median septum in the brachial valve, though somewhat variable, is always over two-thirds the length of the shell. In some individuals the septum has been seen to extend to within 2 mm. of the anterior margin in the brachial valve.

A large subcircular foramen dominates the pedicle umbo, truncating it. Permesothyridid beak-ridges are prominent and border a well marked, extensive interarea.

Internal characters. As for the genus.

REMARKS. This species characterizes the chalk of the *Gonioteuthis quadrata* Zone in the Salisbury district of South Wiltshire and also occurs in the Upper Chalk beds of the same horizon in Hampshire, a fine series of specimens having been collected from excavations for the Southampton Waterworks.

It also occurs in Belgium and has been collected from the Craie de Trivières at Harmignies and Obourg. Specimens have also been found in the Conglomerat d'Obourg and in the base of the Craie d'Obourg.

K. blackmorei differs from *K. pentagulata* (Woodward) in its less acutely convex valves, larger foramen, less produced umbo and more prominent or sharper beak-ridges. It also has a less constricted anterior portion of the shell. In addition, the extensive interarea allows the exposure of the deltidial plates which, in the case of *K. pentangulata*, are usually hidden by a more incurved umbo.

Unlike other species of *Kingena* from the Upper Chalk, the maximum width of the shell in *K. blackmorei* occurs at the posterior end of the shell, giving rise to a more extensive or wider hinge-line.

Dimensions of holotype. 22 mm. long, 21 mm. wide and 13 mm. thick.

Dimensions of paratypes in the Sedgwick Museum Cambridge.

	Length	Breadth	Thickness
B. 65638	19 mm	19 mm	11 mm
B. 65639	21 mm	21 mm	12 mm
B. 65640	17 mm	16 mm	10 mm
B. 65641	19 mm	18 mm	10.4 mm
B. 65642	18.5 mm	17.4 mm	9.9 mm
B. 65643	17 mm	17.5 mm	9.6 mm

Other material used. GSM. 10694 (Institute of Geological Sciences). IG 6292 (Inst. roy. Sci. Belg. Brussels).

Kingena pentangulata (Woodward)

(Pl. 7 figs. 6, 7. Pl. 8, figs. 2–6, Text-fig. 13)

1833 *Terebratula pentangulata* Woodward : 49, pl. 6, fig. 10.
1836 *Terebratula ventroplana* Roemer : 51, pl. 2, fig. 7.
1847 *Terebratula hebertiana* d'Orbigny : 108, pl. 514, figs. 5–10.
1852 *Kingena lima* Defrance ; Davidson : 42, pl. 4, figs. 16, 18, 20.
1901 *Kingena lima* (Defrance) ; Rowe : 64
1904 *Kingena lima* (Defrance) ; Jukes-Browne : 267, 482.
1908 *Kingena lima* (Defrance) ; Rowe : 252.
1961 *Kingena lima* (Defrance) ; Peake & Hancock : 320.

Diagnosis. Large *Kingena*, approximately 16·8 mm. long, 14·4 mm. wide and 9·3 mm. thick. Oval to pentangulate or pentagonal ; plano-convex to biconvex. Rectimarginate to uniplicate. Evenly pustulate. Beak slightly produced, erect to slightly incurved ; beak-ridges poorly defined. Foramen permesothyridid, circular, medium to small. Deltidial plates obscured by incurved beak. Kingeniform loop supported by long median septum.

Neotype. The specimen figured by Woodward (1835 ; pl. 6, fig. 10) from Harford Bridge, Norfolk has been lost. A neotype is therefore proposed from the collections of the Castle Museum, Norwich, registered no. 2060. This is the specimen figured by Davidson (1852, pl. 4, fig. 20) and is part of the Fitch Collection. It is figured here on Pl. 8, fig. 5. Woodward's specimen was collected from one of two pits

working the Upper Chalk at Harford Bridge (Grid. Ref. TG/221057). According to Peake & Hancock (1961 : 336) this locality exposes the top of the Eaton Chalk and part of the Weybourne Chalk, both high in the Senonian and within the broad *Belemnitella mucronata* Zone, Upper Campanian.

In the explanation of Woodward's plate 6, he attributed *Terebratula pentangulata* to Phillips, but there is no evidence in literature that this name was ever used by Phillips for a Terebratulid brachiopod.

Type locality. The locality given for the proposed neotype is Norwich. Although this information might seem somewhat vague, the species is typical of specimens not uncommonly found in the lower part of the *B. mucronata* Zone of the Norwich districts.

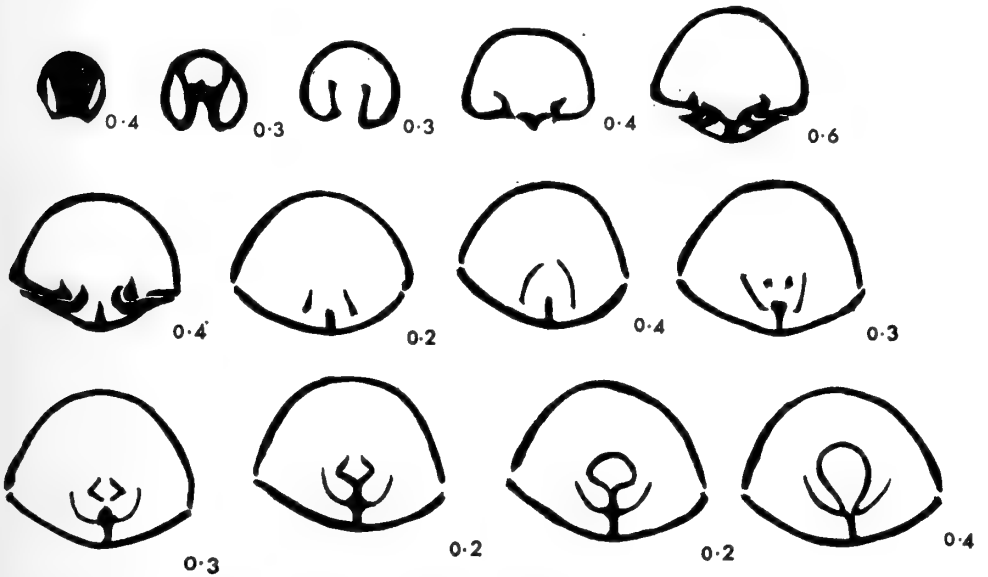


Fig. 13. Serial sections through *Kingena pentagulata* (Woodward) from the Upper Chalk, *mucronata* Zone, Norwich, Norfolk. BB. 45787. ×2.

Description. Young specimens of this species are difficult to recognize and are seldom collected from the Upper Chalk. The ontogeny of the species can be traced, however, by studying the growth-lines on mature, young and intermediate forms. In the early stages of growth, the general outline is subcircular becoming more elongate-oval to pentangulate or pentagonal in maturity. There is a tendency to marginal gerontic thickening and very slight uniplication of the anterior commissure. The maximum width of the species occurs at about half the distance from the umbo to anterior margin, unlike *K. blackmorei* sp. nov. where the maximum width occurs at less than one third the distance from the umbo to anterior margin.

The shell surface is covered with the characteristic pustules of even size and distribution. The punctae are small but fairly widely distributed.

Internal characters. These are essentially as described for the genus with the exception that, as in all Upper Chalk forms, the kingeniform hood is much more developed anteriorly.

Distribution. Records of *Kingena pentangulata* (Woodward) have proved difficult to trace since Davidson (1852 : 42) referred all species of *Kingena* to *K. lima* (Defrance) and references to the species by Rowe (1900, 1901, 1908), Jukes-Browne (1904) and latterly Peake & Hancock (1961 : 320) have been made under the name of *Kingena lima.* However, several fine examples have been examined from the *B. mucronata* Zone, near Salisbury, and two near perfect specimens from the same horizon are in the Sedgwick Museum, B. 5454, B. 5472 and are said to have been collected from the Isle of Wight.

Similarly, continental references have also been to *Kingena lima* (Defrance) and the absence of well documented collections has made the work of defining the distribution of *K. pentangulata* outside British localities very difficult.

In Belgium, the species is not uncommonly found in the Craie d'Obourg at Harmignies, Obourg and Cuesmes and the Craie de Nouvelles at Harmignies, Heure-le-Romain and Ciply. It also occurs in the Craie de Spiennes at Harmignies and Ciply. Here it appears as the typical pentangulate-oval form with the same degree of variation as the Norfolk form. It may also be the species selected and listed by Bosquet (1860 : 390) as *Megerlea pustulosa* from the Upper Chalk of Limburg, but as there is neither description nor illustration upholding this citation it must remain *nomen dubium.*

In France, the species was described by d'Orbigny (1847 : 108, pl. 514, figs. 5–10) as *Terebratula hebertiana* from the Senonian of Chavot and Cezane near d'Ay in the Marne.

Remarks. Rowe (1901 : 64) considered the genus *Kingena* to be represented by one species only within the Upper Chalk, namely *K. lima* (Defrance), but acknowledged the characteristic shape variations within zonal limits, thus, in describing the *B. mucronata* Zone of Dorset (1901 : 24) states " *Kingena lima* here assumes a shape variation which is fully diagnostic of the zone. It is large and pentangulate. These characters begin to appear in the *Actinocamax quadratus* Zone and are notably seen in Dr. Blackmore's series from the Salisbury Chalk . . . " and later " This shape variation is well figured as *Terebratula pentangulata* by Woodward in the ' Geology of Norfolk ' . . . . " In pointing out these characteristic shape variations, Rowe merely emphasizes the subtle differences which separate the forms from the *Gonioteuthis quadrata* Zone, here described as *K. blackmorei* sp. nov., from the species *K. pentagulata* (Woodward). These differences are chiefly confined to beak characters and position of the maximum width of the shell.

Although the length of the median septum in the brachial valve varies from just over half to two-thirds the total length of the shell in this species, it is noticeable that, in the more pentangulate forms where the general outline shows less anterior constriction, the septum is often very much longer, extending to well over two-thirds of the shell length, as in *K. blackmorei.* It is not certain whether this variation in the length of the septum could have any stratigraphical significance. More accurately

collected material at all growth stages must be examined before any suggestion of possible stratigraphical value in this character can be seriously considered.

The oval-pentagonal outline of this species is recognizable as one of the early ontogenetic stages which is maintained in later growth and at all stages throughout its comparatively short stratigraphical range. Variation tends towards a more predominantly oval outline in forms from the higher zones of the Upper Senonian and early Maastrichtian.

Recent work on the stratigraphy of the Cretaceous of Northern Ireland by Mr. Christopher Wood, Institute of Geological Sciences, has added greatly to the records of this species from the Lower and Upper Campanian of County Antrim. Several well preserved typical specimens have been collected from beds equivalent to the basal *mucronata* Zone of Norfolk, as defined by Peake & Hancock (1961), and two specimens, though somewhat atypical in their general outline, have been collected from beds equivalent to those within the Beeston Chalk of Norfolk, Table 1.

Typical examples of *K. pentangulata* have been collected from the core of a boring put down at Port More by the Institute of Geological Sciences. These occurred at depths between 411 and 500 feet and all appeared to be proportionately smaller than examples examined from English localities.

Apart from the localities in Norfolk and Northern Ireland already mentioned, the species has been collected from Studland Bay, Dorset, Coombe Pit and Wool, south Dorset, Alderbury, nr. Salisbury.

Kingena asperulina Stoliczka

1872 *Kingena asperulina* Stoliczka : 28, pl. 7, fig. 14.

EMENDED DESCRIPTION. A large *Kingena*, almost circular in general outline with a slightly produced, suberect umbo. The pedicle foramen is large and circular with well defined permesothyridid beak-ridges bordering an extensive interarea. A slight sulcation develops at the extreme anterior part of the pedicle valve giving rise to faint uniplication. Faint growth-lines and fine pustulate ornament cover the surface of both valves.

HOLOTYPE. G.S.I. no. 1594, Geological Survey of India, Calcutta. Length, 29·50 mm., width, 27·70 mm., thickness, 20·00 mm.

HORIZON AND LOCALITY. Utatur group, north-west Coodycaud, Southern India.

REMARKS. In general outline and size, this species closely resembles the form from the Upper Albian, Red Chalk of Hunstanton, Norfolk, described here as *Kingena spinulosa* (Davidson & Morris). It differs from that species, however, in its slightly more produced beak, more extensive interarea and more evenly convex valves. Since this is the only specimen mentioned and figured by Stoliczka in his original description of the species, it is assumed that there is no paratype material available.

The Utatur group includes beds of both Upper Albian and Cenomanian age, according to the Lexique Stratigraphique International. The Cenomanian beds are appar-

ently commonly exposed in the Coodycaud district but it is not known for certain whether or not the Upper Albian has ever been recorded from this area.

An approximate correlation with European beds of the Cretaceous is given here, Table 2.

Kingena shalanurensis Stoliczka

1872 *Kingena shalanurensis* Stoliczka : 29, pl. 7, figs. 15–17.

EMENDED DESCRIPTION. Distinctly elongate-oval in general outline with even biconvexity of the valves. The short, slightly produced, suberect umbo has fairly distinct but rounded permesothyridid beak-ridges and is dominated by a circular foramen. The hinge-line is narrow, giving the umbo a somewhat terebratulid aspect. A faint sulcus in the anterior part of the pedicle valve gives rise to incipient uniplication of the anterior commissure.

LECTOTYPE. G.S.T. no. 1595, Geological Survey of India, Calcutta, here selected from three syntypes all figured by Stoliczka (1872). The lectotype is the specimen figured by Stoliczka pl. 7, fig. 15.

DIMENSIONS OF LECTOTYPE. Length, 25·50 mm., width, 24·60 mm., thickness, 14·00 mm.

HORIZON & LOCALITY. ? Trichinopoly group. Possibly Lower Senonian, Shalanur, Southern India.

REMARKS. The exact age of this species must remain somewhat uncertain since it is not known from exactly what part of the succession the specimens figured by Stoliczka were collected. According to information taken from the Lexique Stratigraphique International and other sources [Dr. M. K. Howarth, personal communication] the Trichinopoly group embraces beds of Turonian, Coniacian and Santonian age (see Table 2). From the general outlines of the specimens figured on Stoliczka's Pl. 7, figs. 15–17, it is only possible to say that they resemble some variants within the species *Kingena pentangulata* (Woodward) from the British Upper Senonian.

Kingena granulifera Stoliczka

1872 *Kingena granulifera* Stoliczka : 26, pl. 7, figs. 8–12.

EMENDED DESCRIPTION. Elongate-oval to subpentagonal in general outline. Some specimens show a wider hinge-line than others and tend towards less acute anterior constriction, thus giving a subparallel or more rectangular outline with steeply sloping flanks. This form also develops a shallow but noticeable sulcus, beginning about midway from umbo to anterior margin and broadening slightly anteriorly.

LECTOTYPE. G.S.I. 1589, in the collections of the Geological Survey, India, Calcutta.

DIMENSIONS OF LECTOTYPE. Length 18·20 mm., width 14·20 mm., thickness 8·60 mm.

HORIZON AND LOCALITY. Arryalur group, from Olapaudy, Southern India.

Remarks. From the five specimens figured by Stoliczka (pl. 7, figs. 8–12) it is impossible to estimate the full range of variation within the species but they resemble a similar series of specimens of *Kingena mesembrina* (Etheridge) collected from the Gingin Chalk of Western Australia and now in the British Museum (Natural History) nos. BB. 45791–BB. 45795. One of these specimens, BB. 35791, figured here Pl. 6, fig. 8, shows the same subparallel flanks and rectangular general outline as *K. granulifera*. The growth-marks on the shell surface are as pronounced or step-like as those on the figured specimens of *K. granulifera* and a similar extensive, shallow sulcus is also noticeable in the brachial valve. Elliott (1952) redescribed Etheridge's species *Magas mesembrinus* and assigned it to the genus *Kingena*. His illustrations of the species (pl. 1, figs. 1–13) can be compared to the drawings of Stoliczka (1872, pl. 7, figs. 8–12).

It may be that the two species are synonymous, but more material from the Indian locality is needed before any conclusions as to their relationship can be reached.

? *Kingena punjabica* Sahni

1939 *Kingena punjabica* Sahni : 11, pl. 1, figs. 4, 5.

Holotype. G.S.I. Type no. 16637, in the Geological survey of India, Calcutta.

Dimensions of holotype. Length, 16·5 mm., width, 16·5 mm., thickness, 11 mm.

Horizon and locality. The stratigraphical details surrounding this species are somewhat vague and Sahni gives the horizon as ? Neocomian or Upper Jurassic. It was collected from an exposure two and-a-half miles southeast of Pezu, Bannu district, N.W. Frontier Province, Pakistan.

Sahni's figured specimen certainly has external morphological features very similar to those of some *Kingena* species, especially from the Albian and Lower Chalk of England, but, as Sahni states (: 12), the characteristic pustules or granules on the shell surface are missing.

Similar morphological features are noted in the genus *Belothyris* which Smirnova (1960 : 117) described from the Lower Cretaceous of the northwest Caucasus. Examples of this genus have been collected from beds of Lower Cretaceous age at Sheik Budin, near Pezu in the Bannu district of Pakistan by the Geological Survey of Pakistan.

Sahni's *K. punjabica* was collected from the arenaceous beds just above the massive limestone at Sheik Budin. According to Spath (1939 : 136) the ammonites in these beds are Crioceratids similar to those from the *Trigonia swarzi* beds of Tanzania, i.e. Upper Neocomian. The genus *Belothyris*, although originally described from beds of indefinite age, is represented in beds of Upper Neocomian age in France and Switzerland by the species *B. pseudojurensis*.

If, on the other hand, *K. punjabica* is in fact a true *Kingena*, then this would be the earliest record of a species of *Kingena*. However, without proper examination of Sahni's specimen and more details of its brachial loop structure, it is impossible to say for certain as to what genus this species should be assigned. For the present it is assigned broadly to the genus *Kingena*.

Kingena tumida Muir-Wood

1930 *Kingena tumida* Muir-Wood : 34, pl. 5, fig. 7a-c.

HOLOTYPE. No. 14,459 in the collections of the Geological Survey of India, Calcutta and was collected from the Gault of the Samana Range, Punjab.

REMARKS. Adequately described by Muir-Wood (1930 : 34) as an acutely biconvex or globose internal mould with greater convexity of the pedicle valve than the brachial valve. No fold or sulcus are developed and lateral commissures are straight with acutely sloping flanks.

Genus ***BELOTHYRIS*** Smirnova, 1960

TYPE-SPECIES. *Belothyris plana* Smirnova, 1960

DESCRIPTION. The general outline is rounded-pentagonal to elongate-oval, somewhat cinctiform. Acutely biconvex. Rectmarginate to ligate. The slightly produced umbo is suberect to just incurved with a small circular foramen. The permesothyridid beak-ridges are distinct. A high median septum extends to about two-thirds the length of the shell. The shell surface is smooth but the growth-marks are fairly distinct.

Internal characters. Short divergent dental lamellae in pedicle valve support deeply inserted hinge-teeth. Dental sockets with extensive inner and outer socket-ridges. Long shallow hinge-trough giving rise to slender hinge-plates supported by high septum. Descending branches of brachial loop with long inwardly curving crural processes which diminish rapidly. The long septum develops straight, connecting to low transverse band or conical hood from ascending branches.

REMARKS. Smirnova (1960 : 115) suggested that in *Belothyris* there may have been an earlier stage in its development where the individuals had a connection between the descending branches and septum, as in *Kingena*. Although this is a perfectly acceptable idea, in view of recent comparison between species of *Belothyris* and *Kingena* for the present research, it seems more likely that *Belothyris*, *Kingena* and *Zittelina* are products of a common ancestor, possibly from the Middle or Upper Jurassic, which have developed strong individual characters and have remained separate but closely related genera.

RANGE. *Belothyris* is known only from the Lower Cretaceous.

Belothyris pseudojurensis (Leymerie)

(Pl. 9, figs. 1–5, 7)

1842 *Terebratula pseudojurensis* Leymerie : 12, pl. 15, fig. 5, 6.
1847 *Terebratula pseudojurensis* d'Orbigny : 74, pl. 505, fig. 11–16.
1861 *Terebratula pseudojurensis* Leymerie ; de Loriol : 121.
1872 *Terebratula* (*Waldheimia*) *pseudojurensis* Leymerie ; Pictet : 93, pl. 203, figs. 11–15.
1896 *Zeilleria pseudojurensis* (Leymerie) ; de Loriol : 160, pl. 6, fig. 23.

DESCRIPTION. *Belothyris*, elongate-oval to elongate-pentagonal. Ligate anterior commissure. The umbo is slightly produced and the distinct beak-ridges are permesothyridid to a moderate to small, circular foramen. The general outline is cinctiform. Some marginal thickening develops in gerontic stages. In some forms the growth-lines are not particularly distinct, but probably vary with the type of preservation.

NEOTYPE. As the original specimens figured by Leymerie have been lost, and all efforts to obtain a specimen from a French source have failed, a specimen has been chosen from seven specimens collected from the type locality at Marolles (Aube), France and now in the Davidson Collection at the British Museum (Natural History). It is registered as B. 35033 and is figured here, Pl. 9, fig. 3a-c. It is here proposed as neotype for Leymerie's species *pseudojurensis* referred here to the genus *Belothyris*.

REMARKS. There are many forms within the Lower Cretaceous which might very well be assigned to the genus *Belothyris* but there is a need for more research into the internal structure of these forms. Some of the cinctiform specimens collected from the Hauterivian and Valanginian of north Germany and figured by Roemer (1840) may possibly belong to this genus.

Belothyris pseudojurensis appears to be restricted to the French and Swiss Neocomian beds within the Hauterivian.

Belothyris nettletonensis sp. nov.

(Pl. 9, fig. 6a-c)

DIAGNOSIS. Oval to cinctiform. Umbo short, massive. Foramen small, subcircular ; beak-ridges sharp. Deltidial plates exposed. Hinge-line moderately broad ; interarea fairly extensive.

HOLOTYPE. From the Lower Cretaceous, Claxby Ironstone, Nettleton, Lincolnshire in the British Museum (Natural History) registered no. BB. 45788. The specimen was collected by Dr. Peter Rawson.

DESCRIPTION. Medium sized *Belothyris*, 14 mm. long, 12 mm. wide and 9 mm. in thickness. Zeilleriform or cinctiform in general outline. The thin test is smooth and without prominent growth-marks. Marginal thickening is noticeable in the more mature specimens. The anterior commissure is ligate.

REMARKS. The true range of variation cannot be properly ascertained from the very few specimens available but, in general, it is a short *Belothyris* not exhibiting the same degree of anterior sulcation as *B. pseudojurensis* from France and Switzerland which it otherwise resembles.

In England *B. nettletonensis* has been found only in the top beds of the ironstone facies of the Claxby Series at Nettleton, but probably occurs at a similar horizon at Speeton in the Speeton Clay.

MATERIAL. The holotype, BB. 45788 and two other specimens in the British Museum (Natural History) no. BB. 45797–98.

Genus *ZITTELINA* Rollier, 1919

TYPE-SPECIES. *Terebratula orbis* Quenstedt, 1858.

DIAGNOSIS. Oval-pentagonal to subquadrate ; biconvex, smooth. Rectimarginate to incipiently sulcate. Umo short, massive, suberect to slightly incurved ; foramen small, circular ; beak-ridges indistinct, permesothyridid. Brachial loop with double attachment to median septum and expanded band to form kingeniform hood.

DESCRIPTION. Although the type-species is distinctly pentagonal in general outline, the full morphological range of this genus compares favourably with that of *Kingena* from the Cretaceous. Variation within the species, however, does not tend towards elongation of the valves, as in *Kingena*, but towards a broader aspect with increased width of hinge-line. Faint carination of the posterior part of the pedicle valve appears to be present in early development of some species, particularly *Z. orbis* (Quenst.) *Z. impressula* (Quenst.) and *Z. caeliformis* Suess.

Internal characters. The brachial loop, as seen in acid developed specimens from Wurttemburg, shows the characteristic spines on the dorsal surface of the descending and ascending branches as seen in *Kingena* and several genera within the Zeilleriacea from the Middle and Lower Jurassic.

The conical or funnel-shaped kingeniform hood is well developed from the transverse band of the ascending branches but appears to be more quadrate in transverse outline according to serial sections of the type-species, Fig. 14.

A pedicle collar is a marked feature of the pedicle umbo and the same callus infilling of the umbonal cavity is noted which occurs in *Kingena*, *Belothyris* and is also seen in *Waconella* gen. nov.

From the transverse serial sections of the type species, *Z. orbis*, Fig. 14, it is possible to see the marked similarity between the cardinalia and hood attachment in this genus and the same structures in *Kingena*, Fig. 2. The differences between the two genera appear to be confined to the relative angle of the descending branches to median septum which is more acute in *Zittelina*, and the length of the median septum which, in *Kingena*, always extends to well over two-thirds the length of the shell, but remains comparatively short in *Zittelina*, not extending far beyond the point of attachment of the brachial loop.

Zittelina orbis (Quenstedt)

(Pl. 10, fig. 1a-c. Text-fig. 14)

1858 *Terebratula orbis* Quenstedt : 639, pl. 29, fig. 28–38.
1870 *Megerlea orbis* (Quenstedt) ; Zittel : 219, pl. 41, fig. 18.
1871 *Terebratula orbis* Quenstedt ; Quenstedt : 400, pl. 49, figs. 59–61, 63–74.
1883 *Terebratula* (*Waldheimia*) *orbis* Quenstedt ; Engel : 188–213, 230, pl. 5, fig. 7.
1887 *Kingena orbis* (Quenstedt) ; Bukowski : 88.

LECTOTYPE. Here selected, the specimen figured by Quenstedt (1871, pl. 49, fig. 65) from the Upper Jurassic, Middle White Jura, Wurttemburg, Westphalia,

Germany. The specimen is in the Quenstedt Collection at the Institut und Museum für Geologie und Paläontologie, der Universitat, Tübingen, Germany.

DESCRIPTION. *Zittelina* averaging 13 mm. long, 11 mm. wide and 7·9 mm. in thickness. Distinctly oval-pentagonal in general outline. In early growth-stages,

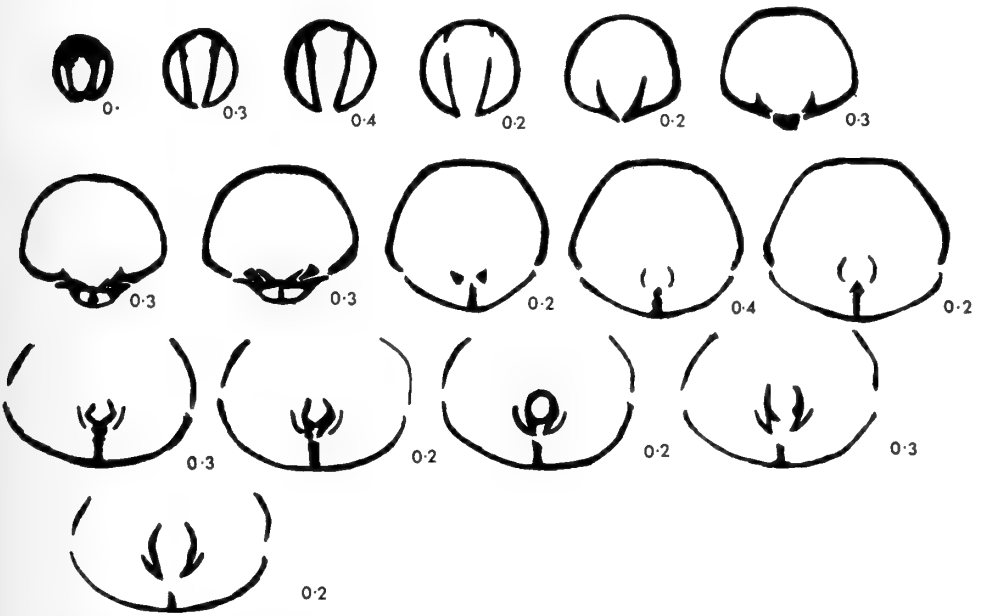


FIG. 14. Series of sixteen transverse serial sections through the umbo of a specimen of *Zittelina orbis* (Quenstedt) from the Upper Jurassic of Wurttemburg, Germany. B. 37717. ×3.

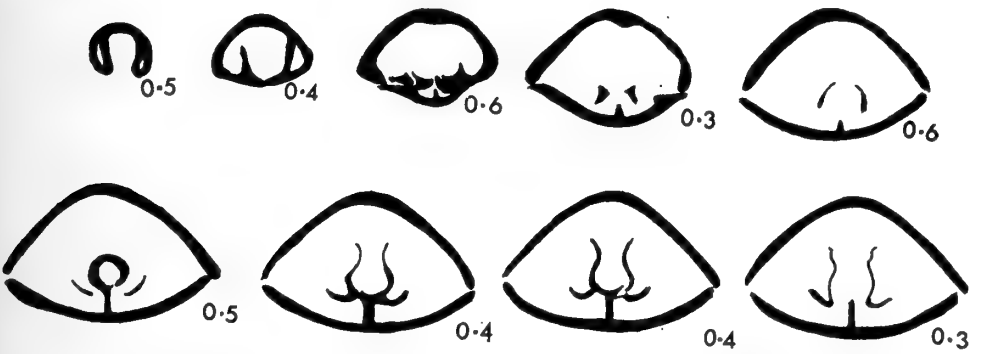


FIG. 15. Series of nine serial sections through the shell of *Frenulina sanguiniolenta* (Gmelin) from off the Philippines, Z.B. 3331 showing similar plan of braccial loop to that of *Kingena* and *Zittelina* but indicating the well formed connecting band of septum to descending branches in the later stages. ×4.

the brachial valve becomes slightly inflated posteriorly and maintains this acute convexity throughout subsequent growth, while the rest of the valve tends to flatten, especially towards the margins. Growth-marks are prominent but are not raised much above the shell surface. The median septum is clearly visible in the brachial valve. Likewise the dental lamellae are distinct as clear lines at the apex of the pedicle valve. The suggestion of a pedicle umbo between the dental lamellae in the pedicle umbo was made by Zittel (1870 : 219) but there is no evidence of such a structure in the serial sections of the type species.

Remarks. *Zittelina orbis* is probably confined to the European continent, but the genus is represented elsewhere. Krumbeck (1905) described two new species and recognized three of Quenstedt's from the Glandarienkalk (Kimmeridgian) of the Lebanon. These were *triangularis* and *latifrons*, which he described as new, and *gutta*, *cubica* and *orbis* of Quenstedt, all of which he assigned to the genus *Kingena*.

Zittel (1870) described a series of beautifully prepared acid developed specimens from South Germany as *Megerlea*. Among these was a specimen of *Z. orbis* (pl. 41, fig. 8a, b) showing most of the characters described here.

Family ***LAQUEIDAE*** Thomson, 1927

Subfamily ***LAQUEINAE*** Thomson, 1927

In the "Treatise", Hatai (1965 : H. 845) proposed the subfamily name Laqueinae for *Laqueus*, ranging from the Miocene to Recent seas. This name had already been used in this context by Thomson (1927 : 256) who proposed it as a subfamily name for *Laqueus* and *Pictothyris*. In view of this oversight, the family name Laqueidae which Hatai also proposed (Hatai, 1965) should therefore be attributed to Thomson 1927 (*nom. transl.*)

Genus ***WACONELLA*** nov.

Type-species. *Terebratula wacoensis* Roemer, 1852

Diagnosis. Evenly biconvex, oval-pentagonal to elongate-oval. Test smooth. Punctae coarse, numerous. Umbo prominent, beak-ridges sharp, interarea extensive ; foramen small, permesothyridid. Deltidial plates conjunct. Anterior commissure rectimarginate. No cardinal process developed. Brachial loop, laqueiniform.

Range. Upper Albian to Lower Cenomanian.

Description. *External characters.* Distinctly terebratulid in general aspect with a small foramen. The smooth exterior is often without any obvious trace of growth-marks, although the mode of preservation may tend to make this character more obvious. Variation within the species is confined to more elongation of the valves to produce a more elongate-oval outline. The interarea and deltidial plates are usually well exposed. Slight labiation of the foramen occurs with gerontic development.

Internal characters. Nothing is known about the early loop development stages of *Waconella* owing to lack of suitable material. Small or young specimens have been sectioned and the serial sections have revealed that the connecting band from septum to descending branches in the small or juvenile individuals is considerably shorter in proportion to the shell than in the more mature forms. This stage is similar to the ultimate stage in the loop development of *Frenulina*.

The adult loop in *Waconella* is virtually the same as in *Laqueus*. The transverse band is broad with a wide central aperture. This aperture is formed by the lateral processes from the transverse band extending towards the descending branches and connecting with them. At this same point, the lateral bands from the septum also connect with the descending branches.

Waconella wacoensis (Roemer)

(Pl. 10 figs. 6a-c, 7a-c ; Text-fig. 16)

1852 *Terebratula wacoensis* Roemer : 81, pl. 6, fig. 2 a, b, c.
1857 *Terebratula wacoensis* Roemer ; Conrad : 147, pl. 3, fig. 1.
1857 *Terebratula leonensis* Conrad : 147, pl. 21, fig. 2a-c.
1901 *Terebratula* (*Kingena*) *wacoensis* Roemer ; Hill : 264, pl. 37, fig. 5, 5a.
1928 *Kingena wacoensis* (Roemer) ; Adkins : 80.
1948 *Kingena wacoensis* (Roemer) ; Cooper : 365, pl. 143, figs. 32–34.
1960 *Kingena wacoensis* (Roemer) ; Perkins : 63, pl. 17, figs. 1–8.

Description. *External characters.* *Waconella* averaging 20 mm. long, 19 mm. wide and 12 mm. in thickness. Subcircular to oval in early growth stages, becoming more elongate-oval in adult stage. Fairly widely spaced, coarse punctae clearly visible. A moderately long median septum is developed in the brachial valve and extends from the apex of the brachial umbo to approximately half the length of the shell. The umbo is slightly produced and is slightly carinate in some individuals. The hinge-line varies from narrow to moderately wide. The beak-ridges are short, fairly distinct and permesothyridid. The foramen is small and circular. A fairly short interarea is reminiscent of that observed in *Laqueus*.

Internal characters. In transverse serial sections through the shell, the posterior portion of the umbonal cavity in the pedicle valve is seen to be infilled with callus which unites the dental lamellae and attaches them to the floor of the valve. Similar infilling of this cavity has been seen in *Kingena*, *Zittelina* and some Recent dallinidae, such as *Macandrevia*.

The cardinalia are in many ways similar to those of *Kingena*, having a broad, fairly shallow hinge-trough, well marked inner and outer socket-ridges and strong, elongate-triangular hinge-plates supported by a strong, high median septum. The hinge-trough flattens anteriorly, giving rise to two ventrally concave plates which lengthen to form long crural processes and the descending branches of the loop. Proceeding anteriorly for a short distance, the descending branches are deflected dorsally and connect with a narrow band from the septum which runs almost horizontal to the floor of the valve. At this point, the connecting band connects or intersects with lateral processes produced from the transverse band of the ascending branches.

The descending branches, therefore, do not close in to meet the median septum, as in *Kingena*, but connect with the septum by means of the interconnecting band, as in *Laqueus*. The mature loop develops further down the shell or more anteriorly than it does in *Kingena* where the loop develops maturity at the posterior end of the shell.

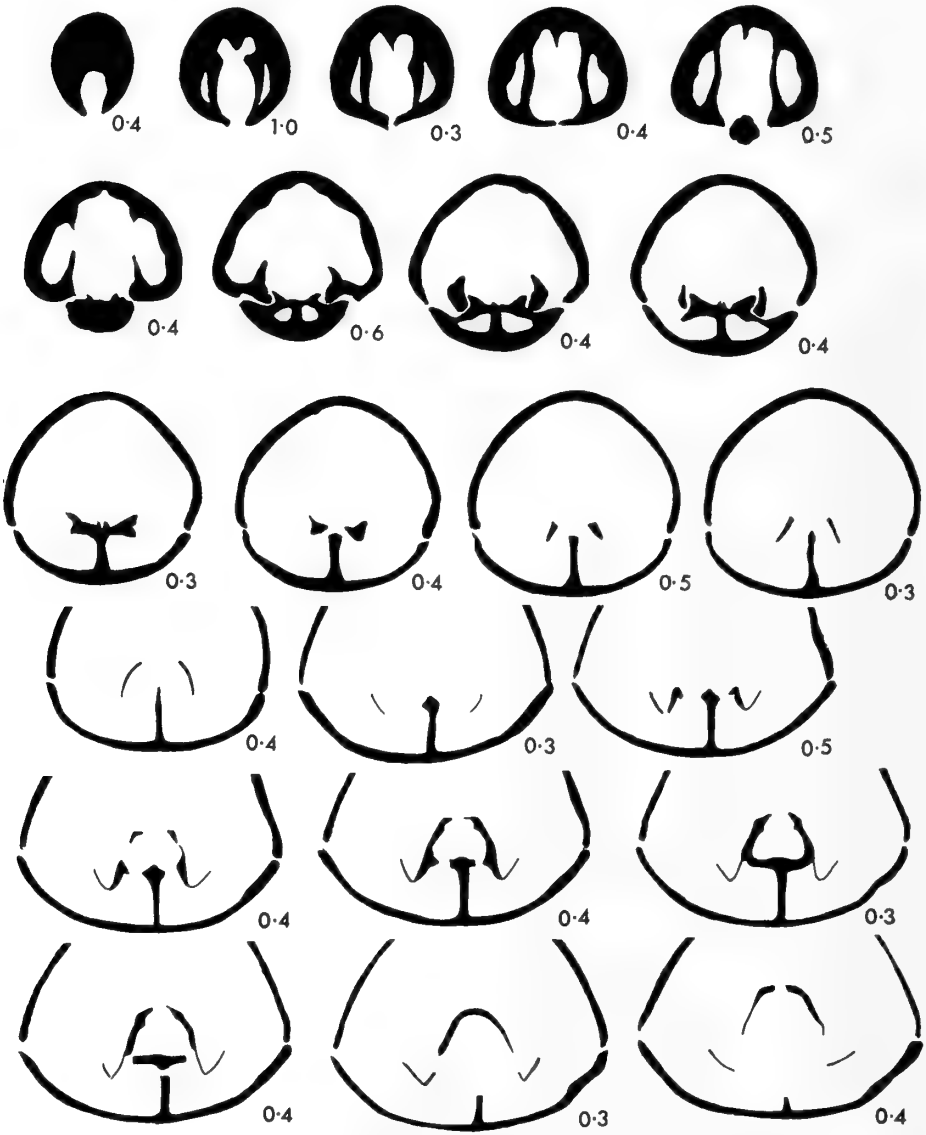


FIG. 16. Series of twenty-two serial sections through *Waconella wacoensis* (Roemer), Duck Creek Formation, Texas, showing similar loop and connecting bands to those of *Laqueus californicus* (Koch) as seen in Fig. 17. BB. 5718. ×4.

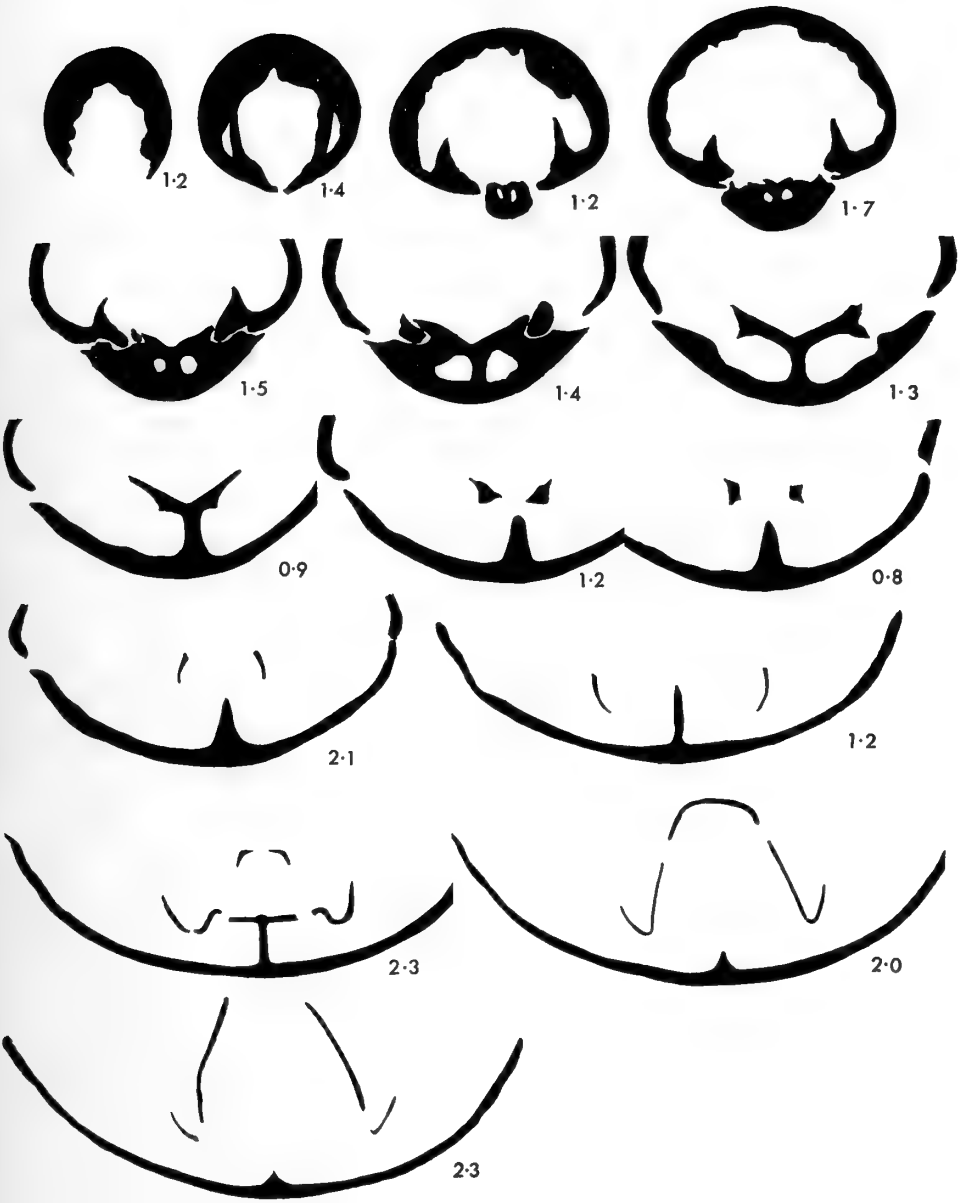


FIG. 17. Fifteen serial sections through the shell of *Laqueus californicus* (Koch) from Recent seas, for comparison with sections of *Waconella wacoensis* (Roemer) in Fig. 16. Z.B. 3332. ×2 approx.

REMARKS. *Waconella wacoensis* has been recorded from practically every locality where the Washita strata are exposed. It has been recorded from many localities in central and western Texas, occurring in the Comanchean Series from the Edwards and Georgetown Formations, from the Grayson Marl, Del Rio Shale, Main Street limestone, Pawpaw Shale, Weno Marl, Denton Marl, Fort Worth Limestone, Duck Creek Formation and the Kiamichi Formation. In terms of European stratigraphy, it covers beds from Upper Albian to Lower Cenomanian age. (see Table 3 : 40). It abounds in beds of this age in Texas and is frequently found at the same horizon in Cretaceous deposits in Mexico.

CONCLUSIONS

The present geological range of the Dallinidae is considered to be from the Upper Trias to Recent seas, but there are many more genera which may belong to this family still to be thoroughly investigated.

In 1959, Dagis described the genus *Aulacothyropsis* from the Upper Trias of Siberia and figured a series of transverse sections of the type species *A. reflexa* (Bittner). These sections show characters which are remarkably similar to those of the Cretaceous genus *Kingena* and also to the Recent genus *Frenulina*. It may be possible to trace the lineage of these forms in the course of time and throw some more light on their evolution. In the meantime, however, there are many intermediate forms still to be investigated. Some of these are the terebratellacean genera within the Middle and Upper Jurassic which are known only from mature adult specimens and very often from their external morphology alone.

The attainment of a kingeniform loop may be expected to occur more than once in the family Kingenidae, for the mechanism of loop-development and evolution suggested by Elliott (1953) explains a similar phenomenon in the superfamily Terebratellacea generally, in which the Kingenidae belongs. Thus the future investigaton of the Jurassic forms mentioned above may clarify the relationship, if any, of *Aulacothyropsis* to *Kingena*.

The genus *Rugitela* described by Muir-Wood (1936) from the Fuller's Earth Rock of Somerset and now known to have a more extensive range from Middle Jurassic to Lower Cretaceous, shows signs of early loop attachment to septum, possibly dallinoid stages, which are in need of further investigation. Likewise, the genus *Tamarella* described by Owen (1965) from the Upper Aptian of southern England requires more detailed research on early stages in view of its possible relationship to *Psilothyris*, which Cooper described from the Lower Cretaceous of Arizona, before its proper place in the classification can be established. Similarly, the genus *Digonella*, described by Muir-Wood (1934) from the Bathonian, may also have early dallinoid stages as suggested by that author in her classic work.

All this depends very much on the discovery of very young forms which might show early loop developmental stages. Such specimens are difficult to find and are not often recognized even when they have been collected. Perhaps with more painstaking and more critical observation of small specimens already in collections it will be possible in time to fill the existing gaps in our knowledge of this fascinating group of brachiopoda.

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PLATE 1

All specimens are reproduced at ×2 except where otherwise stated. a = dorsal view. b = lateral view. c = anterior view.

Kingena lemaniensis (Pictet & Roux)

FIG. 1a-c. LECTOTYPE. Lower Albian, Grand Bornand, France. G.M. CB. 2530.

FIG. 2a-c. Lower Albian, Shenley Limestone, Shenley Hill, Leighton Buzzard, Bedfordshire. B.M. BB. 45796.

FIG. 3a-c. Lower Albian, Shenley Limestone, Shenley Hill, Leighton Buzzard, Bedfordshire. B.M. BB. 45799.

FIG. 4a-c. Lower Albian, Shenley Limestone, Shenley Hill, Leighton Buzzard, Bedfordshire. B.M. BB. 54800.

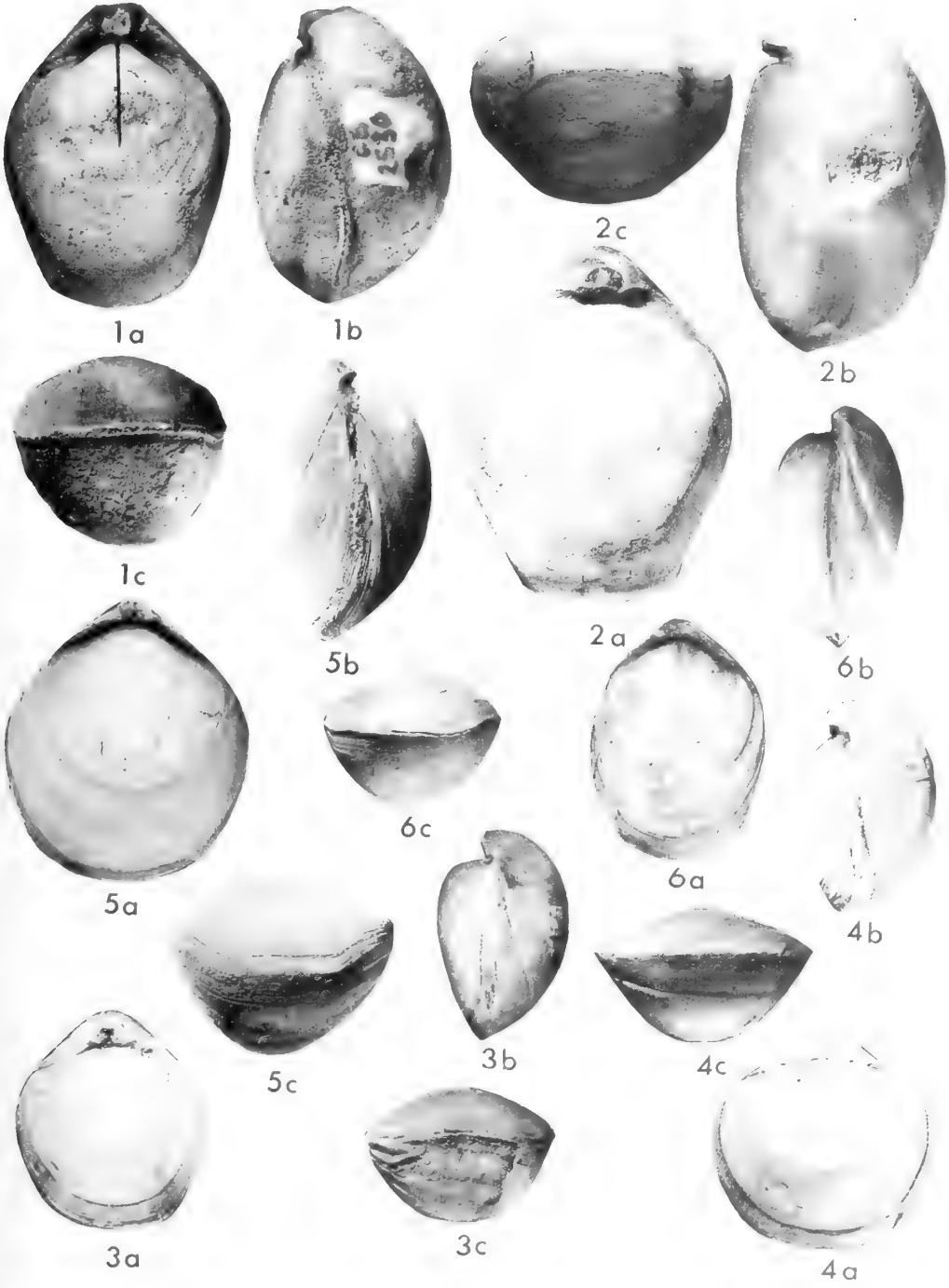
Kingena convexiformis (Walker)

FIG. 5a-c. Lower Albian, Shenley Hill, Leighton Buzzard. B.M. B. 26388.

Kingena convexiformis (Walker)

FIG. 6a-c. Lower Albian, Shenley Hill, Leighton Buzzard. B.M. B. 26379.

The prefix G.M. = Muséum d'Histoire Naturelle, Geneva.
B.M. = British Museum (Natural History).


1a
1b
2c
2b
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5b
6b
6c
5a
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4b
5c
3b
4c
3a
3c
4a

PLATE 2

Kingena spinulosa (Davidson & Morris)

FIG. 1a-c. Upper Albian, Red Chalk, Hunstanton Cliff, Norfolk. B.M. B. 25382.

FIG. 2a-c. Upper Albian, North Grimston, Yorkshire. B.M. B. 25413.

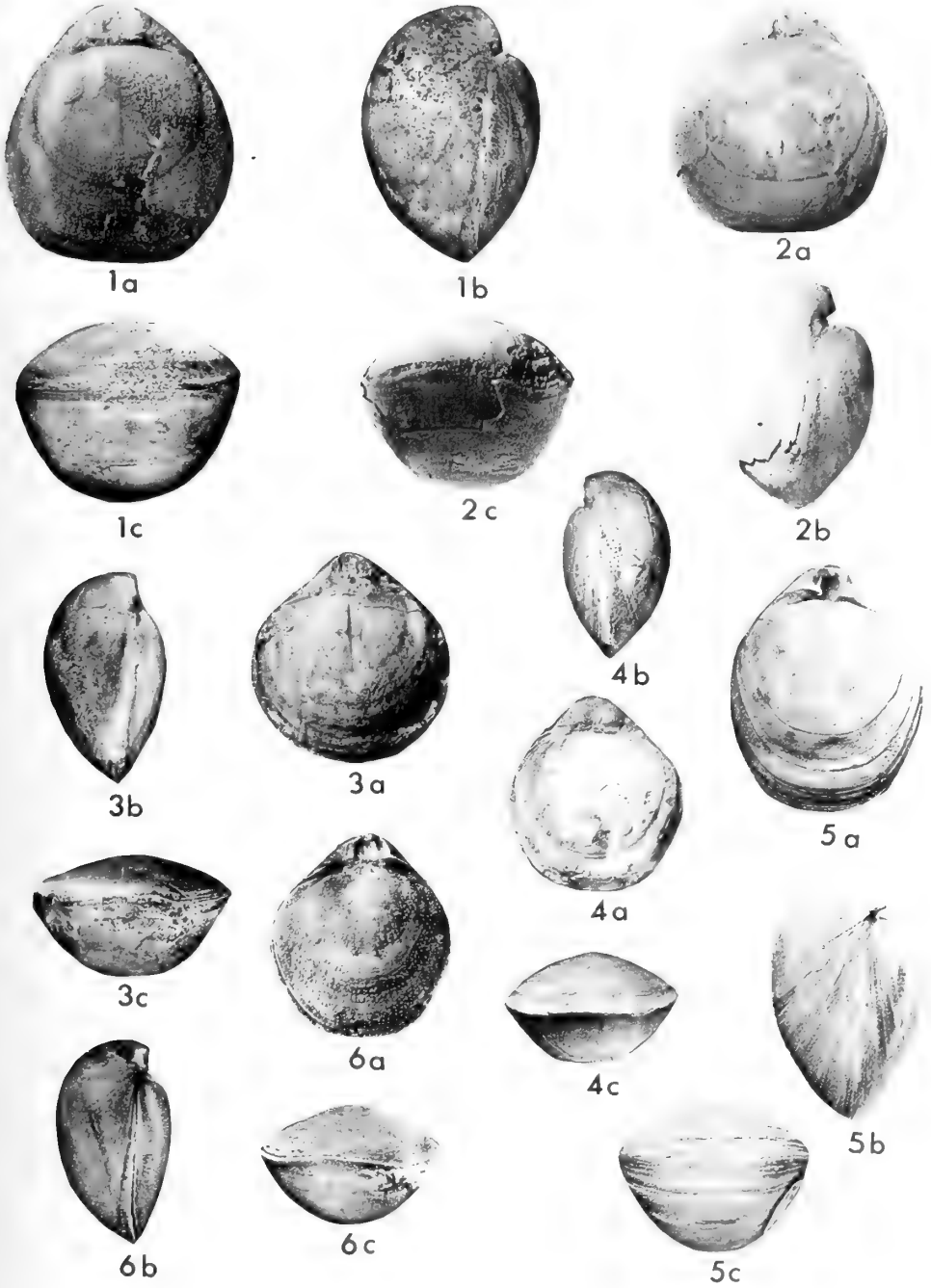
FIG. 3a-c. Upper Albian, Red Chalk, Hunstanton, Norfolk. B.M. B. 5255.

FIG. 4a-c. Upper Albian, Red Chalk, Hunstanton, Norfolk. B.M. BB. 45802.

FIG. 5a-c. HOLOTYPE. Upper Albian, Gault, (Bed 10 of Price), Copt Point, Folkestone, Kent. B.M. B. 5260.

FIG. 6a-c. Upper Albian, Gault, (Bed 10 of Price), Folkestone, Kent. B.M. B. 3296.

Prefix B.M. = British Museum (Natural History).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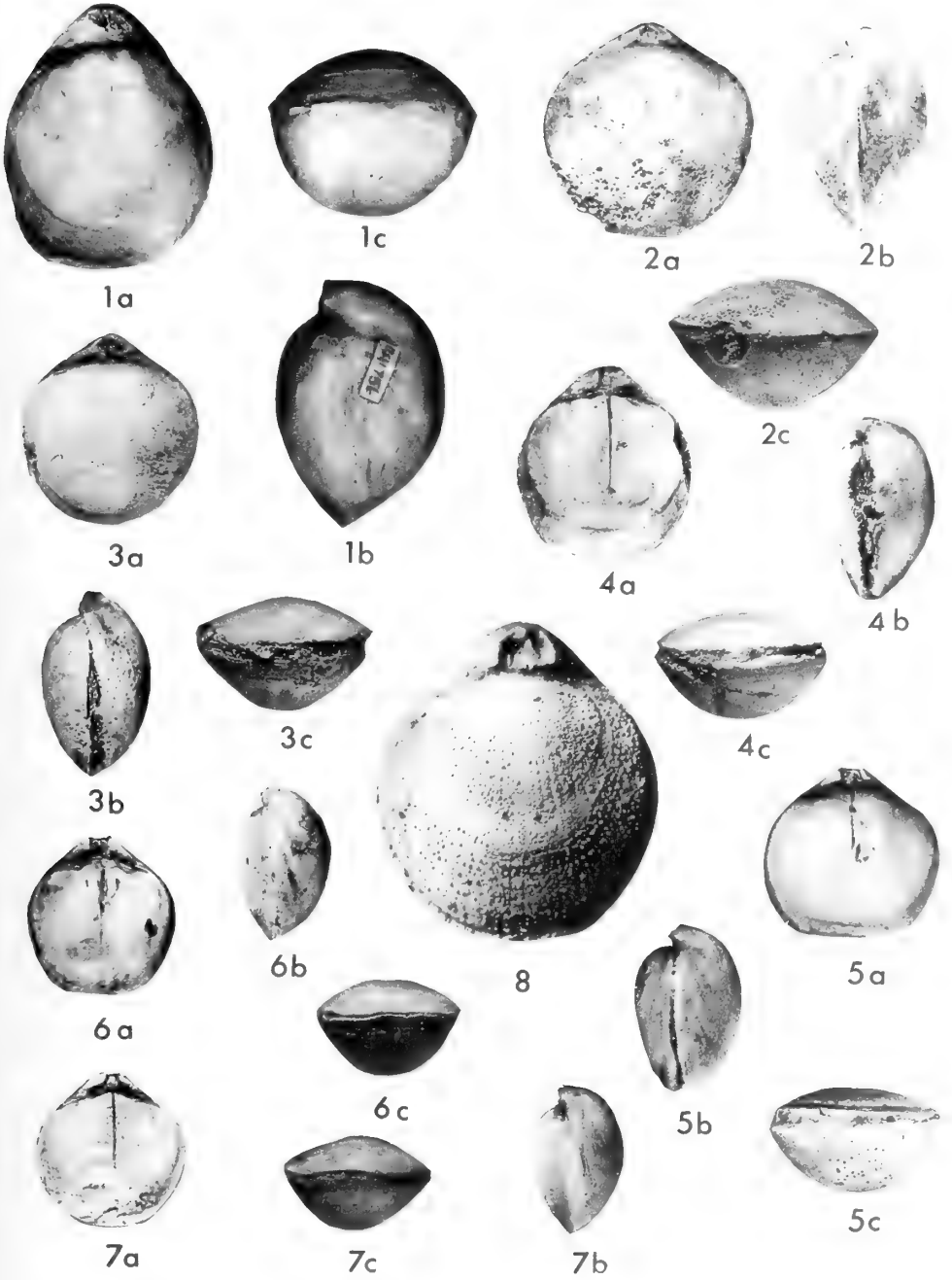
6c
5c

PLATE 3

Kingena spinulosa (Davidson & Morris)

FIG. 1a-c. Upper Albian, Red Chalk, Hunstanton, Norfolk. S.M. B. 41756.
FIG. 2a-c. Upper Albian, Red Chalk, Hunstanton, Norfolk. B.M. BB. 45803.
FIG. 3a-c. Upper Albian, Red Chalk, Hunstanton, Norfolk. B.M. BB. 45804.
FIG. 4a-c. Upper Albian, (Derived), Cambridge Greensand. B.M. B. 22915.
FIG. 5a-c. Upper Albian, (Derived), Cambridge Greensand. B.M. B. 22915.
FIG. 6a-c. Upper Albian, (Derived), Cambridge Greensand. B.M. BB. 45806.
FIG. 7a-c. Upper Albian, (Derived), Cambridge Greensand. B.M. BB. 45807.
FIG. 8. Enlarged view of specimen from Bed 10, Gault, Folkestone showing pustules seemingly following the line of the striae. ×4. B.M. B. 3296.

Prefix B.M. = British Museum (Natural History)
S.M. = Sedgwick Museum, Cambridge.


1a
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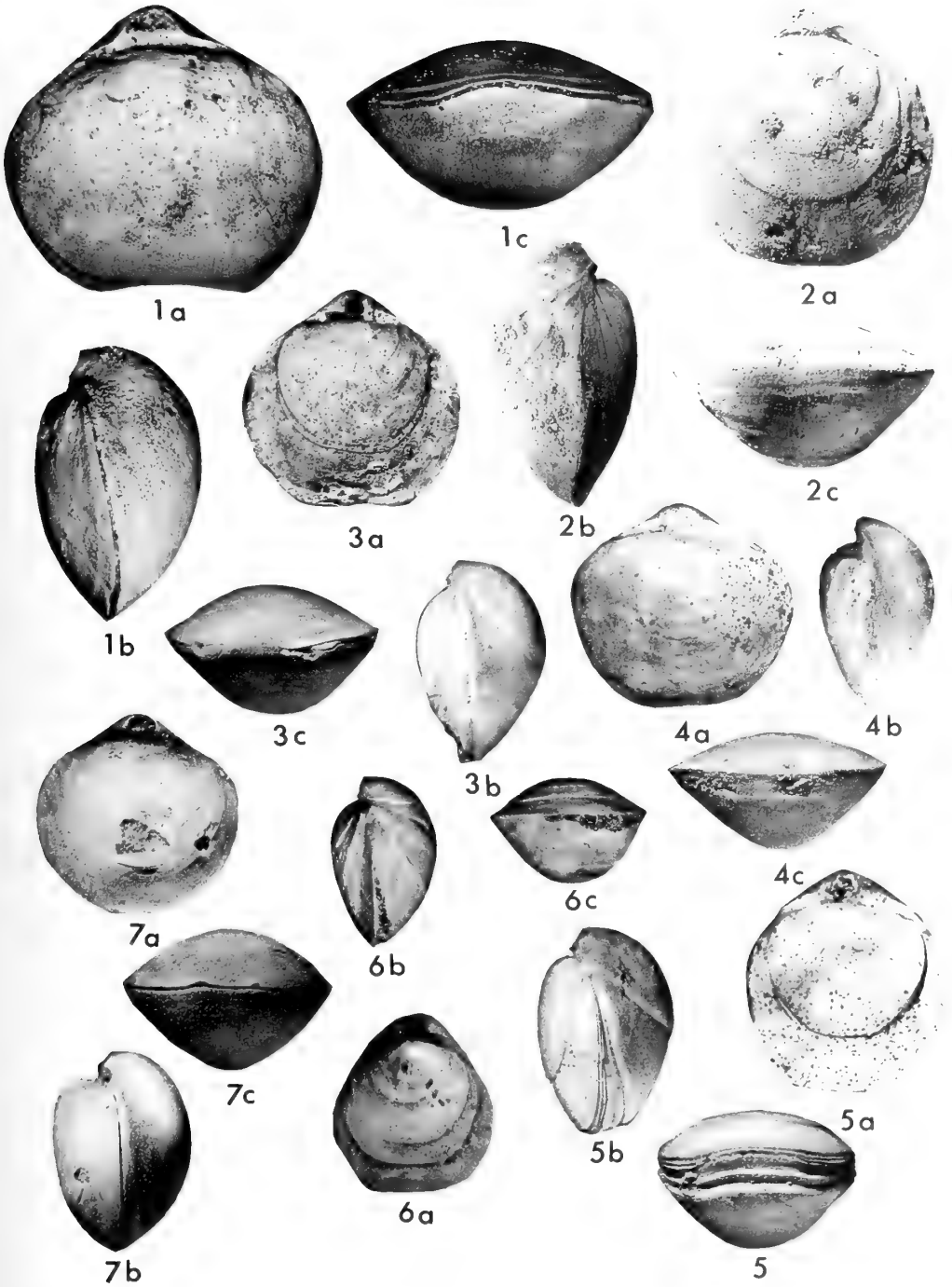
6c
5b
7a
7c
7b
5c

PLATE 4

Kingena arenosa (d'Archaic)

FIG. 1a-c. Upper Greensand, Warminster, Wilts. B.M. no. 88760.
FIG. 2a-c. Upper Greensand, Warminster, Wilts. B.M. B. 491.
FIG. 3a-c. Tourtia, Tournai, Belgium. NEOTYPE. I.G. 8261.
FIG. 4a-c. Middle Cenomanian, Cap le Heve, Normandy, France. B.M. BB. 45808.
FIG. 5a-c. Middle Cenomanian, Le Marchand, Normandy. I.G. Unregistered duplicate.
FIG. 6a-c. Upper Greensand, Warminster, Wilts. B.M. no. 23260.
FIG. 7a-c. Middle Cenomanian, Le Marchand, Normandy. I.G. Unregistered duplicate.

Prefix B.M. = British Museum (Natural History).
I.G. = Institut royal Soc. Sciences Belgique, Brussels.


1a
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3c
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4b
7a
6b
6c
4c
7c
5b
5a
6a
7b
5

PLATE 5

Kingena arenosa (d'Archaic)

FIG. 1a-c. Tourtia, Tournai, Belgium. I.G. 5096a.

FIG. 2a-c. Middle Cenomanian, Montignies-sur-Roc, Belgium. B.M. B. 35456.

FIG. 3a-c. Tourtia, Tournai, Belgium. I.G. 5096b.

FIG. 4a-b. Middle Cenomanian, near Le Havre, Normandy. N.H.P. 6503 d'Orbigny Collection.

FIG. 5a-c. Middle Cenomanian, Montignies-sur-Roc, Belgium. B.M. B. 85103.

Kingena concinna sp. nov.

FIG. 6a-c. Middle Cenomanian, Dover, Kent. B.M. BB. 3434.

FIG. 7a-c. HOLOTYPE. Middle Cenomanian, *rhotomagense* Zone, (Bed 5 of Price), between Folkestone and Dover, Kent. B.M. B. 93758.

FIG. 8a-c. Middle Cenomanian, *rhotomagense* Zone, between Folkestone and Dover, Kent. B.M. B. 93795.

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N.H.P. = Muséum d'Histoire (Nationale) Naturelle, Paris.
I.G. = Inst. roy. Sci. Belgique, Brussels.

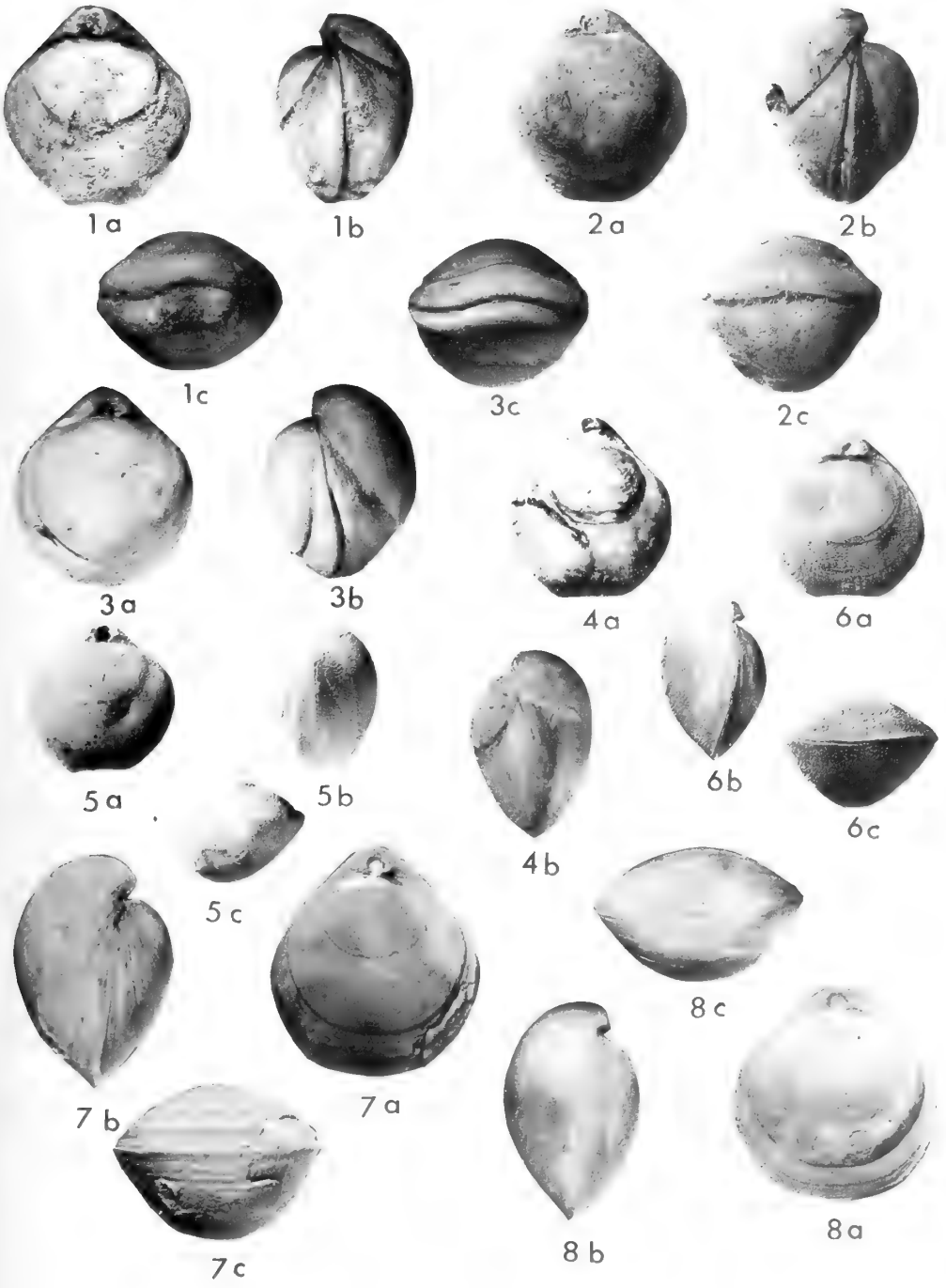
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PLATE 6

Kingena elegens sp. nov.

FIG. 1a-c. Turonian, *H. planus* Zone, Reed Quarry, nr. Royston, Hertfordshire. C. Wood Collection.

FIG. 2a-c. Turonian, Galeriten-Schichten, Graes, nr. Ahous, Germany. B.M. BB. 45780.

FIG. 3a-c. HOLOTYPE. Turonian, *H. planus* Zone, Boswell, Lincs. B.M. B. 55241.

Kingena concinna sp. nov.

FIG. 4a-c. Middle Cenonanian, *rhotomagense* Zone, Dover, Kent. B.M. B. 93760.

FIG. 5a-c. Middle Cenomanian, Cherry Hinton, Cambridge. S.M. B. 21166.

FIG. 6a-c. Cenomanian, Cambridge Greensand (indigenous). B.M. B. 49680.

Kingena lima (Defrance)

FIG. 7a-c. (elongated variety) *M. coranguinum* Zone, Thanet Coast, Kent. B.M. B. 79704.

FIG. 8a-c. Typical form. *Marsupites* Zone, Foreness Point, Margate, Kent. B.M. BB. 45809.

FIG. 9a-c. ***Kingena mesembrina*** (Etheridge), Gingin Chalk, Western Australia. B.M. BB. 45791.

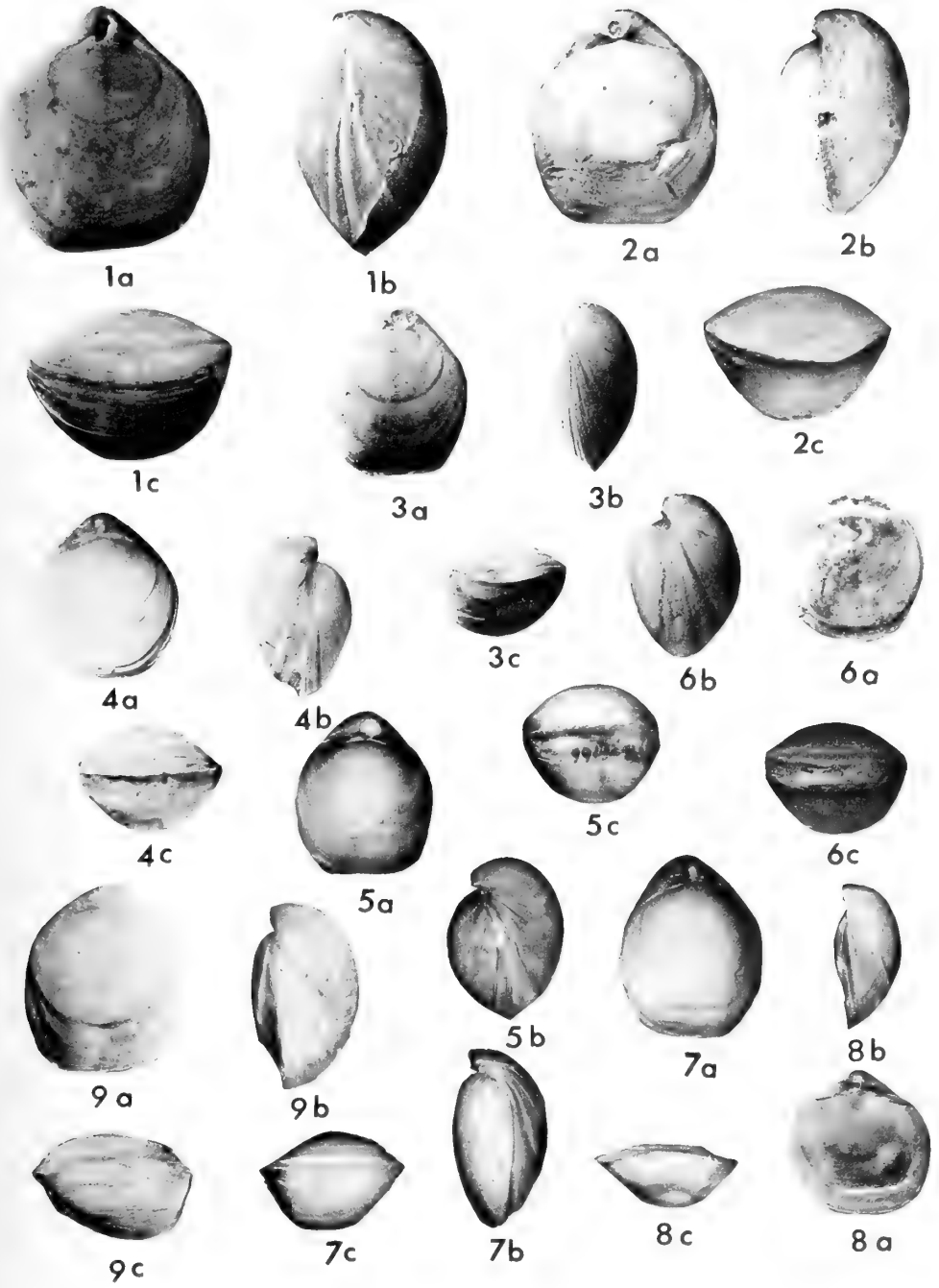
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PLATE 7

FIG. 1a-c. ***Kingena blackmorei*** sp. nov. Upper Chalk, *Gonioteuthis quadrata* Zone, Southampton. S.M. B. 65639.

FIG. 2a-c. HOLOTYPE. ***Kingena blacokmorei*** sp. nov. *G. quadrata* Zone, East Harnham, nr. Salisbury, Wiltshire. B.M. B. 92779.

FIG. 3a-c. ***Kingena blackmorei*** sp. nov. *G. quadratus* Zone, Southampton, S.M. B. 65642.

FIG. 4a-c. ***Kingena lima*** (Defrance) NEOTYPE, Upper Chalk, *Marsupites* Zone, Foreness Point, Margate, Kent. B.M. B. 79709.

FIG. 5a-c. ***Kingena lima*** (Defrance), Upper Chalk, *M. coranguinum* Zone, Thanet Coast, Kent. B.M. B. 79704.

FIG. 6. ***Kingena pentagulata*** (Woodward), Ur. Chalk, *mucronata* Zone, Freshwater, Isle of Wight. S.M. B. 5454.

FIG. 7a-c. ***Kingena pentagulata*** (Woodward), Upper Senonian, *mucronata* Zone, near Norwich, Norfolk. B.M. BB. 45458.

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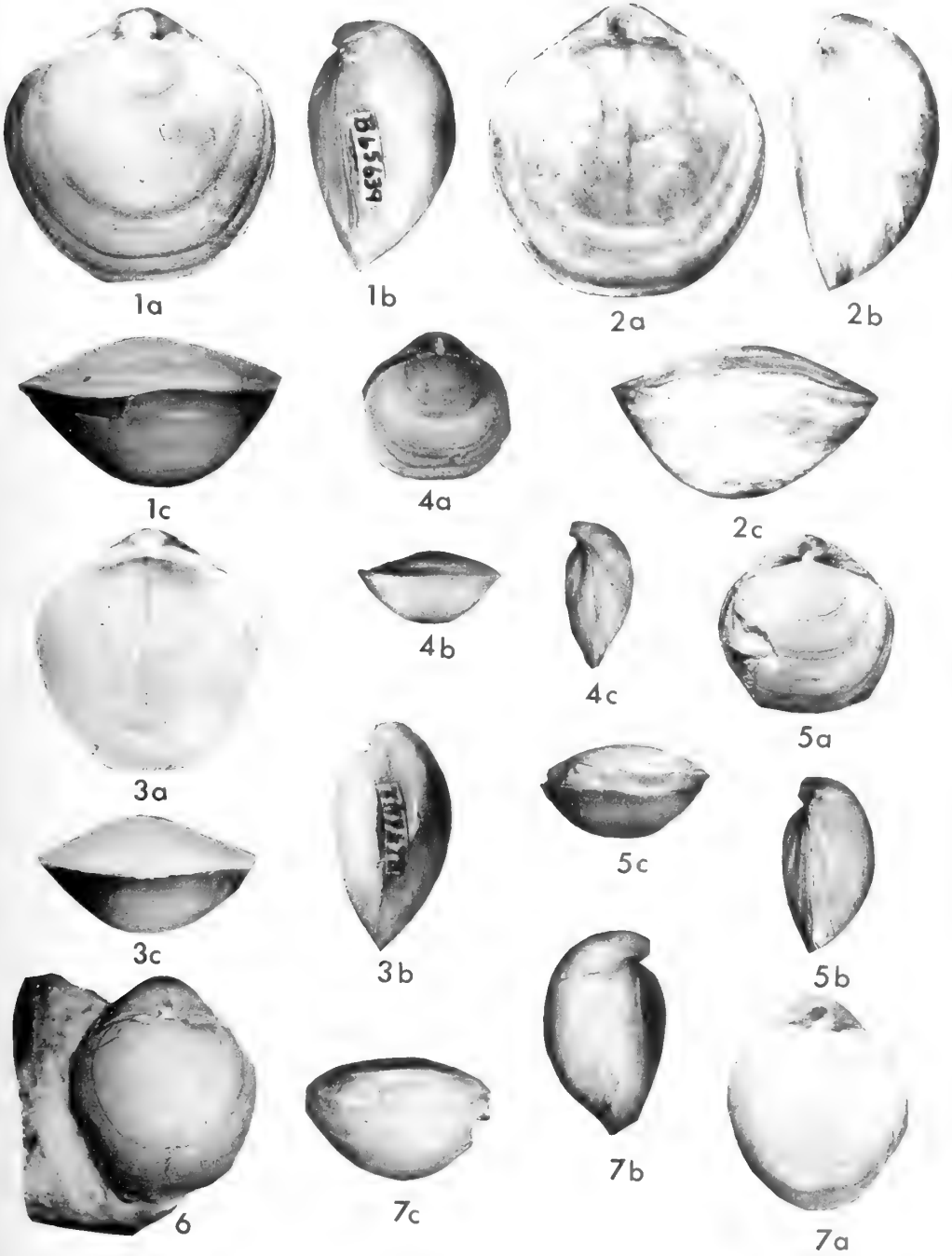
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PLATE 8

FIG. 1a-c. ***Kingena blackmorei*** sp. nov., Base of Craie d'Obourg, Harmignies, Belgium. I.G. 8261.

FIG. 2a-c. ***Kingena pentangulata*** (Woodward), Craie de Nouvelles, Ciply, Belgium. I.G. 8084.

FIG. 3a-c. ***Kingena pentangulata*** (Woodward), Craie d'Obourg, Obourg, Belgium. I.G. 5496.

FIG. 4a-c. ***Kingena pentangulata*** (Woodward), Upper Senonian, *mucronata* Zone, Norwich, Norfolk. B.M. BB. 45810.

FIG. 5a-c. ***Kingena pentangulata*** (Woodward), NEOTYPE. No. 2060, Norwich Castle Museum. Fitch Collection, collected from the *mucronata* Zone, Norwich.

FIG. 6a-c. ***Kingena pentangulata*** (Woodward), Ur. Senonian, Epernay, France. B.M. B. 5259.

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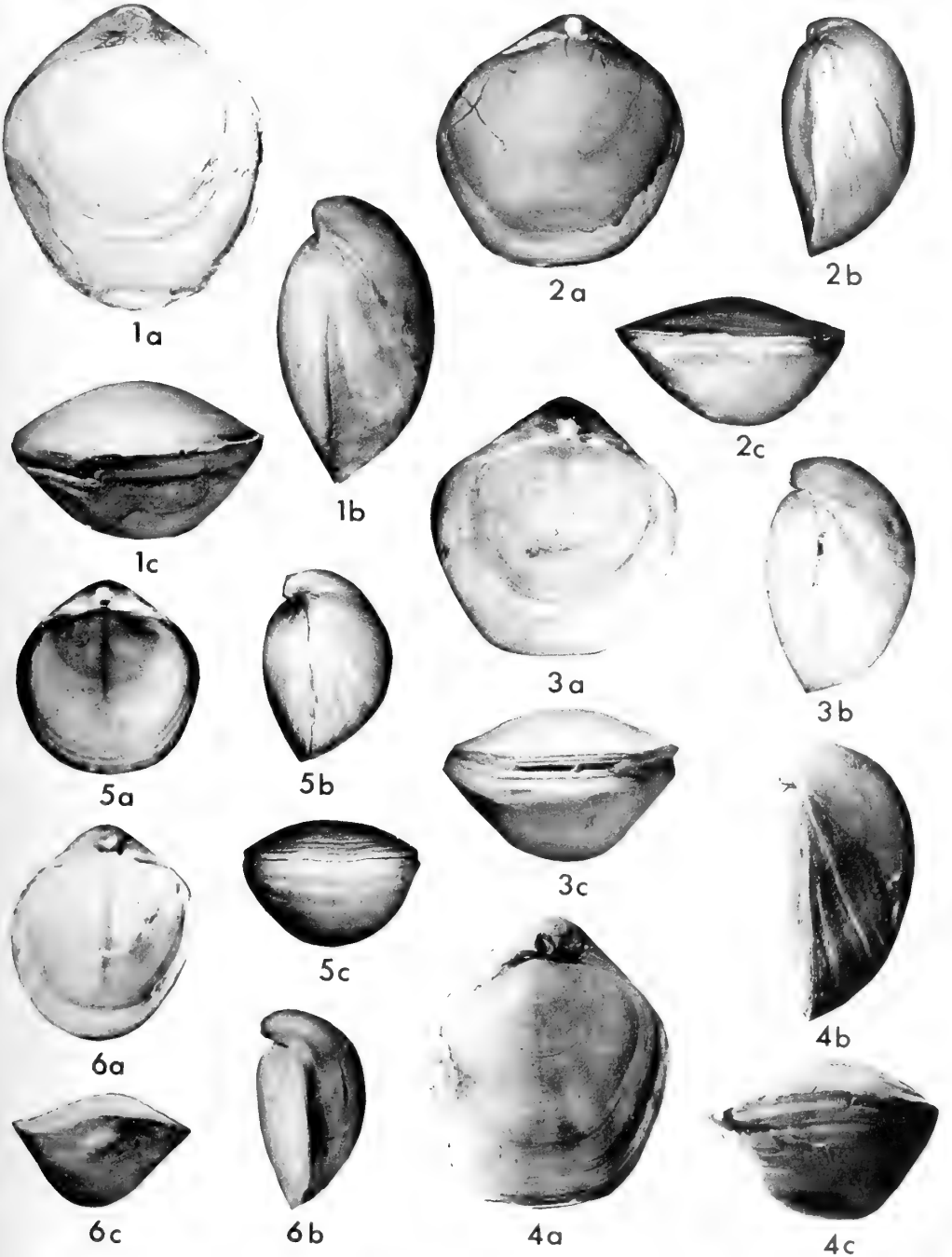
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PLATE 9

Belothyris pseudojurensis (Leymerue)

FIG. 1a-c. Hauterivian, Marolles (Aube), France. B.M. B. 35035.

FIG. 2a-c. Hauterivian, Marolles (Aube), France. B.M. B. 8612.

FIG. 3a-c. Hauterivian, Marolles (Aube), France. NEOTYPE B.M. B. 35033.

FIG. 4a-c. Hauterivian, Marolles (Aube), France. B.M. B. 6756.

FIG. 5a-c. Neocomian, Le Clape, (Aude), Southern France. B.M. B. 35040.

FIG. 6a-c. HOLOTYPE. ***Belothyris nettletonensis*** sp. nov. Claxby Ironstone, Nettleton, Lincolnshire. P. Rawson Collection, B.M. BB. 45788.

FIG. 7a-c. Hauterivian, Le Landeron, Switzerland. B.M. B. 42271.

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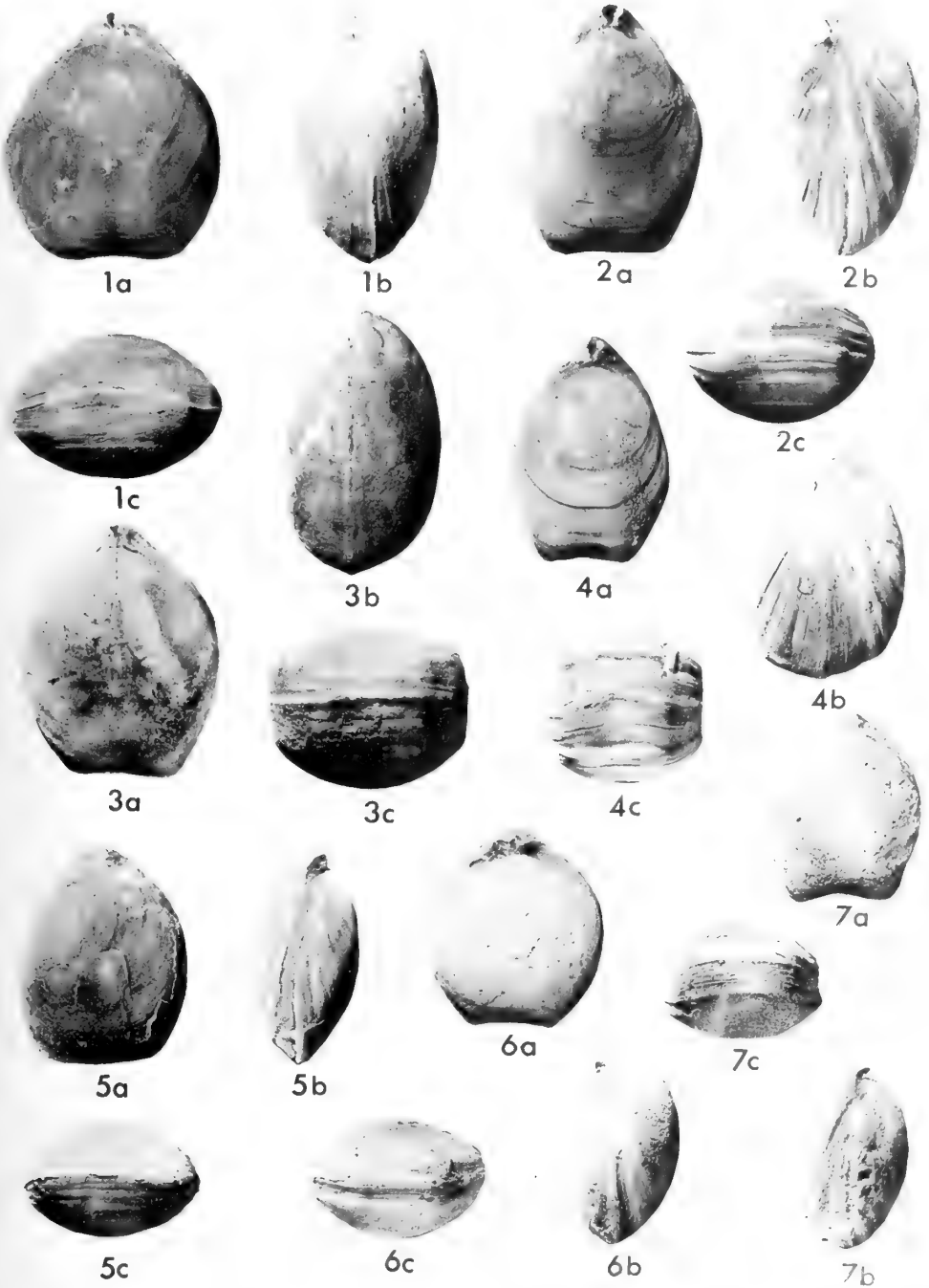
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PLATE 10

FIG. 1a-c. ***Zittelina orbis*** (Quenstedt), Upper Jurassic, White Jura, Wurttemburg, Germany. B.M. B. 37717.

FIG. 2a-c. ***?Kingena punjabica*** Sahni, Lower Cretaceous, Pezu, Bannu district, Pakistan. B.M. BB. 18816.

FIG. 3a-c. ***Belothyris plana*** Smirnova, Lower Cretaceous, N.W. Caucasus, U.S.S.R. B.M. BB. 45460.

FIG. 4a-c. ***Belothyris marianoviensis*** Smirnova, Lower Cretaceous, N.W. Caucasus, U.S.S.R. B.M. BB. 45461.

FIG. 5a-c. ***Belothyris regularis*** Smirnova, Lower Cretaceous, N.W. Caucasus. B.M. BB. 45459.

FIG. 6a-c. ***Waconella wacoensis*** (Roemer) gen. nov. Comanchean, Main Street Formation, Tarrant Co., Texas, U.S.A. B.M. BB. 5708.

FIG. 7a-c. ***Waconella wacoensis*** (Roemer) gen. nov. Comanchean, Duck Creek Formation, Texas, U.S.A. B.M. BB. 57016.

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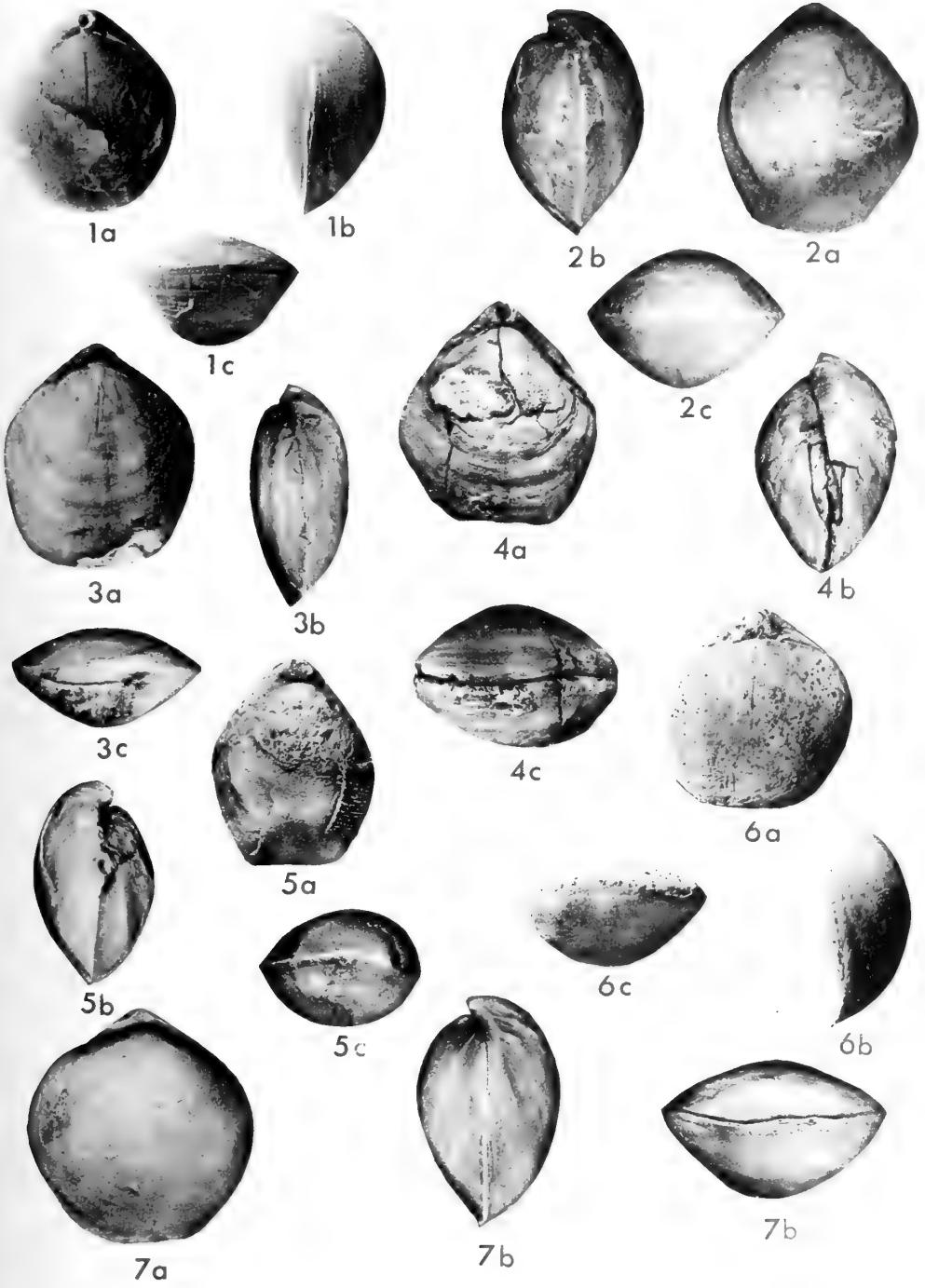
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PLATE 11

FIG. 1. ***Kingena pentangulata*** (Woodward), Upper Chalk, Norwich. Anterior view of dissected loop to show attachment points to median septum. B.M. B. 4927. ×5.

FIG. 2. As above. Ventral view showing kingeniform hood.

FIG. 3. ***Zittelina impressula*** (Quenstedt), Upper Jurassic, White Jura, γ, Grafenburg, Bavaria, Germany. Anterior view of acid developed loop showing points of attachment to septum and lateral spines. B.M. B. 45092. ×6.

FIG. 4. As above. Ventroanterior aspect showing extensive hood and attachment to septum. ×6.

FIG. 5. ***"Kingena" alcocki*** Joubin, Recent Seas, off Travancore, India. Ventral view showing relatively thin bands connecting loop to septum. B.M. ZB. 491. ×5.

FIG. 6. As above, to show the broad laqueiniform hood. ×5.

FIG. 7. ***Hamptonina buckmani*** (Moore), Middle Jurassic, Great Oolite, Hampton Down, Bath. Showing early pre-campagiform stage in loop development. B.M. BB. 42937. Approximately. ×12.

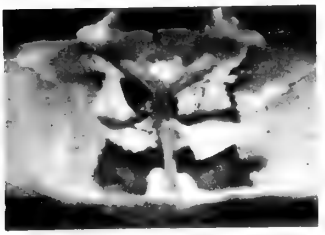
FIG. 8. As above. Early campagiform stage. (Broken loop). B.M. BB. 42939. ×15.

FIG. 9. As above. Campagiform stage. Sponge-Coral Bed, Bathampton Down, Somerset. B.M. BB. 10228. ×20.

FIG. 10. ***Kingena pentangulata*** (Woodward), Upper Senonian, *mucronata* Zone, Norwich, Norfolk. B.M. BB. 45782. Early pre-campagiform stage. ×20.

FIG. 11. As above. Early campagiform stage. B.M. BB. 45783. ×15.

FIG. 12. As above. Campagiform stage. B.M. BB. 45466. ×15.



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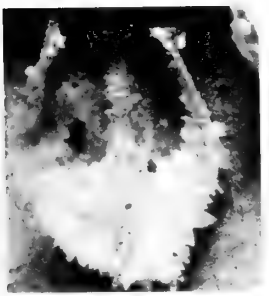

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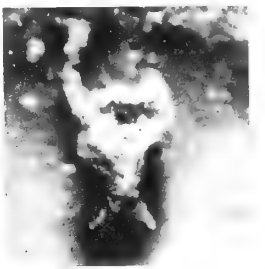

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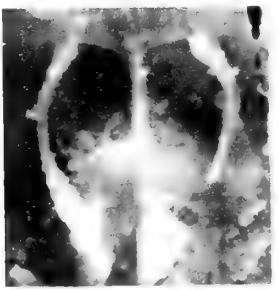

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PLATE 12

FIG. 1. Shell mosaic pattern of ***Kingena lima*** (Defrance), from the Upper Chalk, Marsupites Zone, Margate, Kent. ×650.

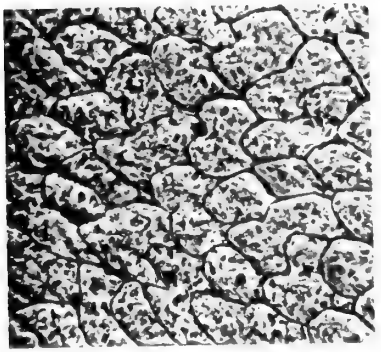
FIG. 2. Shell mosaic of ***Terebratella dorsata*** (Gmelin) from Recent Seas, showing distribution of endopunctae. X650.

FIG. 3. Shell mosaic of ***Kingena lemaniensis*** (Pictet & Roux) from the Lower Albian, Shenley Hill, Leighton Buzzard, Bedfordshire, showing the relative size of an endopuncta. ×660.

FIG. 4. Shell mosaic of ***Campages basilanica*** Dall, from a position just anterior of muscle scar in the brachial value. ×680.

FIG. 5. Shell mosaic of ***Kingena spinulosa*** (Davidson & Morris) from the Gault, Bed 10 of Price, Folkestone, Kent. ×675.

FIG. 6. Shell mosaic of ***Macandrevia cranium*** (Muller) from Recent seas, showing the distribution of the numerous endopunctae. ×650.



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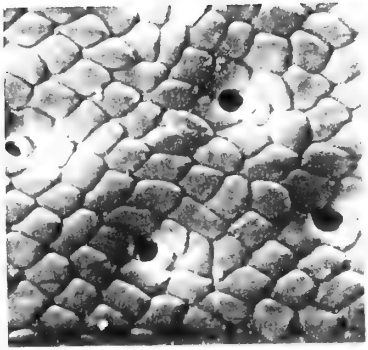

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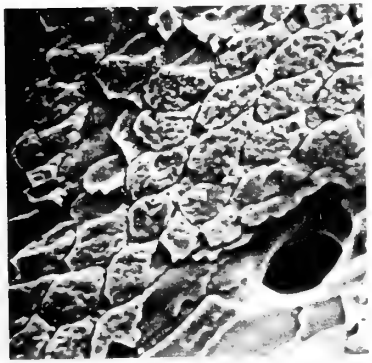

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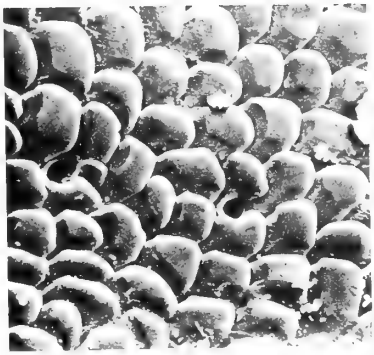

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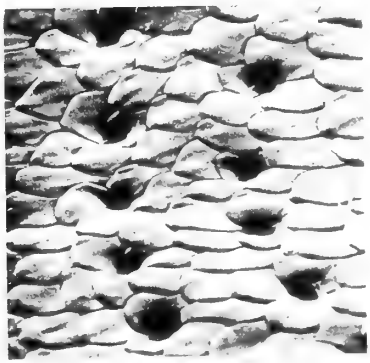

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PLATE 13

FIG. 1. Shell mosaic of ***Laqueus californicus*** (Koch) from a position near the lateral margin of the pedicle value. ×650.

FIG. 2. ***Lacqueus vancouverensis*** (Davidson), shell mosaic from a position in the brachial valve just anterior of muscle scar. ×620.

FIG. 3. Pustulate shell ornament of ***Kingena pentangulata*** (Woodward), Upper Senonian, Norwich, showing the regular size and even distribution of the pustules. B.M. B. 92793. ×15.

FIG. 4. 'Stereoscan' micrograph of surface of shell of ***Kingena spinulosa*** (Davidson and Morris) from the Gault, Folkestone, showing the uneven distribution and irregular size of pustules. B.M. B. 45801. ×20.

FIG. 5. Longitudinal section through shell of ***Kingena pentangulata*** (Woodward), Upper Senonian, Norwich, showing pustule composed of more finely granular primary shell material. B.M. B. 92778. ×200.

FIG. 6. Section of same specimen showing puncta penetrating the shell and involving the secondary shell fibres. ×200.

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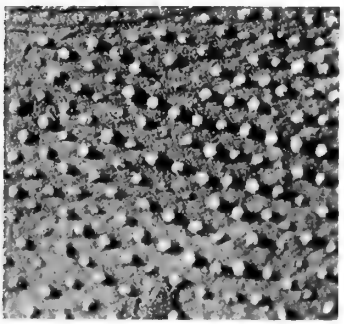

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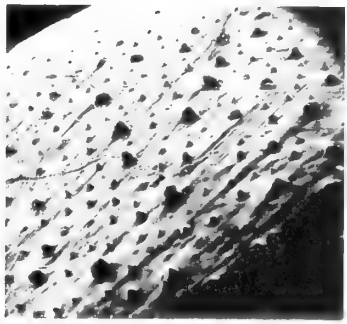

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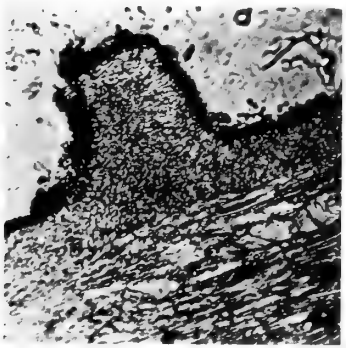

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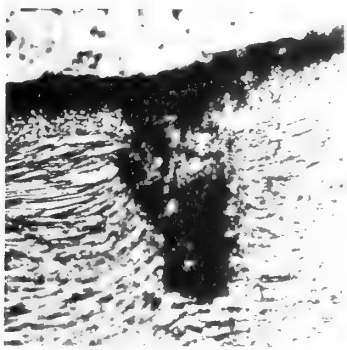

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PLATE 14

FIG. 1. Enlargement of umbo of ***Kingena pentangulata*** (Woodward), Upper Senonian, Norwich. B.M. B. 5261. × 10.

FIG. 2. Enlargement of umbo of ***Kingena elegens*** sp. nov. Turonian, Lincolnshire. × 10.

FIG. 3. Enlargement of umbo of ***Kingena arenosa*** (d'Archaic) from the Cenomanian of Warminster, Wiltshire. × 10. B.M. B. 8268.

FIG. 4. Enlargement of umbo of ***Kingena blackmorei*** sp. nov. from the Upper Senonian of Salisbury, Wiltshire. × 10. B.M. BB. 45826.

FIG. 5. ***Kingena pentangulata*** (Woodward), Upper Chalk, Norwich. Young individual showing the fine spines attached to the brachial loop. B.M. BB. 45465. × 10.

FIG. 6. ***Rugitela waltoni*** (Davidson) from the Inferior Oolite, Le Monsard, Roche, France. Showing similar arrangement of spines on brachial loop. B.M. BB. 3210. × 5.

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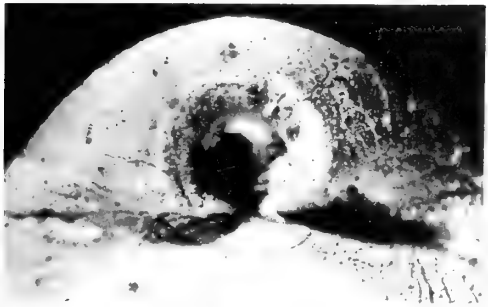

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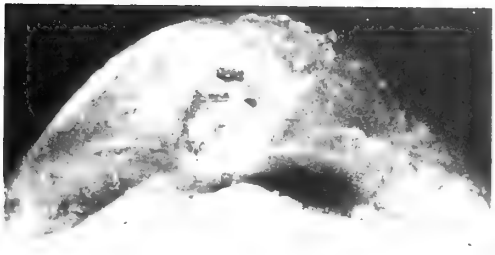

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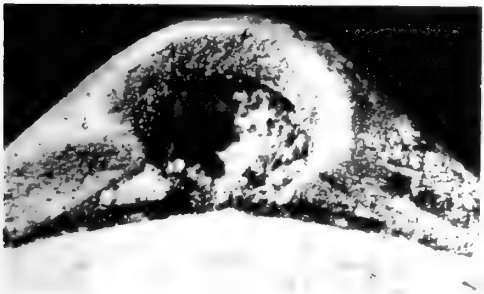

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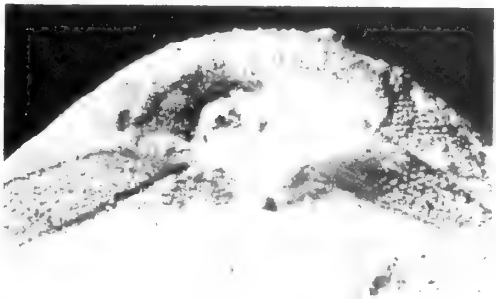

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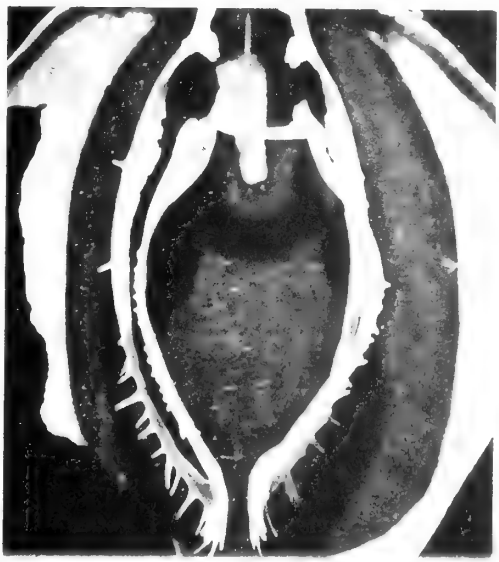

A RECONSIDERATION OF THE EAST INDIAN LETTER CLASSIFICATION OF THE TERTIARY

BY
CHARLES GEOFFREY ADAMS

Pp. 85–137; 3 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 19 No. 3
LONDON: 1970

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A RECONSIDERATION OF THE EAST INDIAN LETTER CLASSIFICATION OF THE TERTIARY

By C. G. ADAMS

CONTENTS

		Page
I.	Introduction	87
II.	Acknowledgements	90
III.	General observations on the letter classification	90
	(a) Historical background and comparison with European stage terminology	90
	(b) Difficulties of inter-regional correlation	92
	(c) The facies problem	92
IV.	Remarks on the stratigraphical chart and range chart	94
	(a) The stratigraphical chart	94
	(b) The range chart	99
V.	Notes on the stages and stage boundaries	100
VI.	Notes on the marker foraminifera	109
VII.	Problems and conclusions	126
VIII.	References	131

ABSTRACT

The East Indian Letter Classification of the Tertiary is re-examined and extended to cover the entire Indo-West Pacific region between latitudes 40°N. and 40°S. Carbonate sediments spanning the interval Upper Palaeocene to Recent are used to indicate where faunal assemblages typical of each Letter Stage have been found. Problems of regional correlation, facies, and stage boundaries are discussed. The ranges of the known marker foraminifera are plotted, and are considered individually in the text.

I. INTRODUCTION

The Letter Classification is a means of dividing the Tertiary of the East Indies into a number of parts or " stages ", each of which is characterized by an assemblage of larger foraminifera. In its original form, six main divisions were recognized (van der Vlerk & Umbgrove 1927). These were subsequently increased to eight (Leupold & van der Vlerk 1931), but later were once again reduced to six (van der Vlerk 1955). Tertiary *a* is the oldest division and Tertiary *h* the youngest; they are usually written *Ta*, *Tb*, etc. This rather broad classification was improved by dividing certain stages into numbered parts corresponding to the ranges of species or to the occurrence of particular generic assemblages. Tertiary *e* was divided into five parts (Te_{1-5}) by

Leupold & van der Vlerk, largely on the supposed ranges of species of *Spiroclypeus*. Unfortunately, these early attempts at refinement proved premature since the ranges of the various species had not then been established satisfactorily. Later workers such as Rutten (see van Bemmelen 1949 : 87), Mohler (1949) and Eames *et al.* (1962) produced their own versions of the Letter Classification and in so doing helped to improve the original scheme, but no one has re-examined the premises on which the classification was based or has tried to put it on a firmer foundation.

The Letter Classification was erected because of difficulties encountered when the conventional stage terminology of Europe was applied to successions in the Far East. These difficulties arose because the molluscan and foraminiferal faunas were different in the two regions. The faunas of the tropical and subtropical Indo-Pacific proved to be richer and more varied than those of Europe and the Mediterranean, particularly in post-Eocene times. There were, however, enough similarities between the faunas for broad correlations to be possible (thus it was soon realized that T*a*/*b* = Palaeocene+Eocene, and that T*b* alone = Upper Eocene), although the dissimilarities caused great confusion at stage level.

The Letter Stages have never been typified by strata, and although Leupold and van der Vlerk indicated the main areas and sections in which the stage faunas had then been recognized, they did not suggest that one locality was more important than another for defining any particular stage. It is now known that the foraminiferal faunas of the East Indies are not peculiar to the area but are widespread over the entire Indo-West Pacific, which region, for the purpose of this paper, is defined as comprising the Indian Ocean and its bordering lands, the East Indies, the western seaboard of the Pacific Ocean and the Pacific Isles between 40°N. and 40°S. There is no virtue in considering the Letter Classification only in the context of the East Indies, especially as some divisions of the Tertiary are poorly developed in that area.

A decade ago, it seemed probable that the Letter Stages could be correlated fairly accurately with the European stages, and some workers (e.g., Glaessner 1959) felt that the Letter Classification had outlived its usefulness. At that time most stratigraphers were using only a limited number of the available European stage names, and there appeared to be a wide measure of agreement regarding their meaning. Thus, Aquitanian and Burdigalian were thought to be synonymous with Lower Miocene (Eames *et al.* 1962). The fact that the stratotypes of many European stages (e.g., Aquitanian and Burdigalian) contained no larger foraminifera in common with their supposed age-equivalents in the Far East was overlooked as it was thought that a satisfactory inter-regional correlation was possible by means of faunas known from the Middle East. The advent of correlation by planktonic foraminifera changed this view. Following a series of papers by authors such as LeRoy (1952) and Blow (1956), a zonal scheme for the Tertiary, founded on planktonic foraminifera, was proposed by Bolli (1959). This zonation, although based on the faunas of Trinidad, was soon seen to be of world-wide importance. Within a short time, stratotype sections in Europe were being re-examined for planktonic foraminifera, and strata typical of the Letter Stages were reinvestigated in the Indo-Pacific. The results were not always immediately helpful. Certain European sections were found to be barren of plankton (e.g., the type Helvetian) or to contain only restricted planktonic

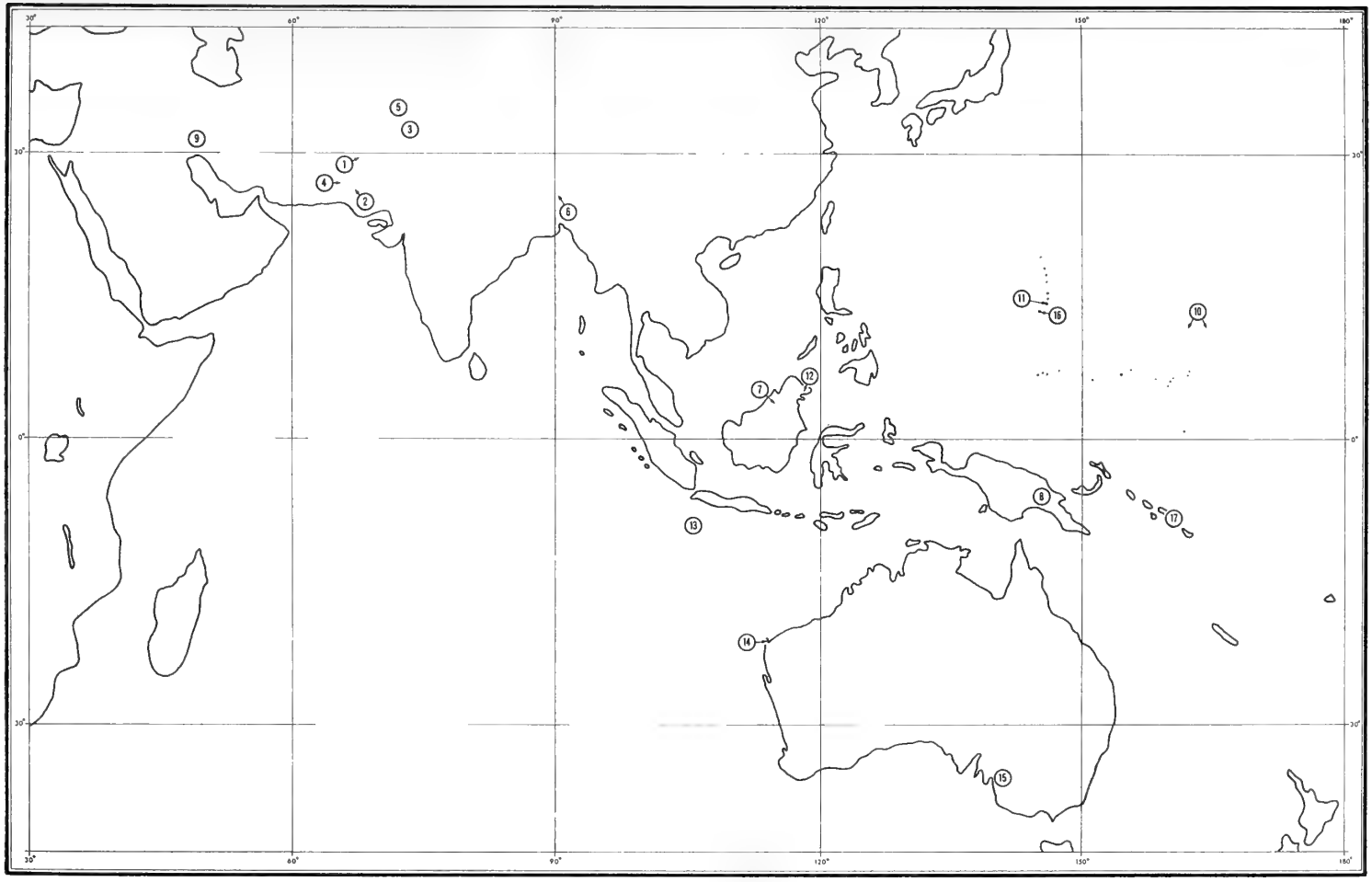


FIG. 1. **Map** showing the relative geographical positions of the successions illustrated in Figure 2.

assemblages (e.g., Chattian). Some stratotype sections included only a small number of plankton zones (Aquitanian and Burdigalian) or were found to be lateral equivalents of one another (Bormidian and Aquitanian *s.l.*). In the Indo-Pacific it was found that faunas previously thought to be age-equivalents of particular European stages (e.g., Tf_{1-2} and Burdigalian) were, in fact, different.

Since its first appearance, the planktonic zonal scheme has been revised and extended by Banner & Blow (1965), by Bolli (1966) and by Blow (1969). Banner and Blow employ a different terminology from that of Bolli, and the two versions differ in various other respects. However, both schemes have their merits, and both can be applied throughout the tropical and subtropical zones. It is generally acknowledged that planktonic zonation has greatly improved Tertiary correlation and further improvements may be expected in future. Unfortunately, plankton is not always present in marine strata, and when it occurs it may be indeterminable or undiagnostic. There are thus many places where great thicknesses of sediment can be dated only by means of larger foraminifera, and it is important to bring the dating of these successions into line with those in which plankton has been found.

The purpose of this paper is to revise the Letter Classification (a) by giving it a more objective stratigraphical basis (b) by reconsidering the faunal assemblages typical of each stage, and determining, as far as possible, the ranges of the marker genera and species (c) by considering the nature and significance of the stage boundaries. It is hoped that by improving this classification and drawing attention to its strengths and weaknesses, it will be possible to relate it more accurately to the European stages and to the planktonic zonal schemes, thus, paradoxically, contributing to its eventual abandonment in favour of a single system of universal applicability.

II. ACKNOWLEDGEMENTS

The author is indebted to his colleague, Dr. D. D. Bayliss, to Dr. W. J. Clarke (British Petroleum Company) and to Dr. B. K. Samanta (University of Calcutta) for information, useful discussions and for reading the first draft of the paper. He is grateful to Professor W. Storrs Cole (Cornell University) who kindly criticized a later version of the typescript and made many helpful suggestions. His thanks are also due to Dr. F. E. Eames and Professor L. Hottinger for valuable discussions and information, and to Mr. R. L. Hodgkinson for technical assistance.

This paper was written at the request of the Malaysian Geological Survey (Borneo Region), to whose geologists the writer is indebted for assistance in the field.

III. GENERAL OBSERVATIONS ON THE LETTER CLASSIFICATION

(*a*) *Historical background and comparison with European terminology*

The background of research and publication against which the Letter Classification evolved was very different from that which existed in Europe when the Tertiary epochs and stages were first described. Palaeontologists and stratigraphers, usually employed by oil companies and mining concerns, worked under considerable difficulties and had neither the time nor the facilities to complete detailed faunal and stratigraphical studies such as were commonplace elsewhere. Indeed, some workers

were actively discouraged from publishing their results for commercial reasons. Papers published by palaeontologists in Europe on the basis of material sent to them from the East Indies, usually contained little or no useful stratigraphical information —for none was available to the authors. The arduous field conditions in the tropics, difficult terrain, and shortage of trained staff, meant that problems arising from reconnaissance surveys could not easily be solved, whilst verification of anomalous results was virtually impossible. The introduction of the Letter Classification, provided a simple but effective way of dividing up Tertiary time by utilizing fossils that even non-specialists could quickly learn to identify, and despite its imperfections, it has for many years satisfied a need that could not have been met in any other way.

The main features of the European stages and the East Indian Letter Stages are compared below.

European stages	*Letter stages*
1. Based on a section or sections in a specified locality or area.	Based on assemblages of larger foraminifera thought to be characteristic of particular divisions of Tertiary time.
2. Type sections were, or could be, designated.	No type sections exist.
3. Total fauna and flora of stratotype available for investigation.	Nothing available.
4. Further collecting from stratotypes usually possible.	Further collecting impossible.
5. Ranges of marker fossils theoretically determinable by reference to stratotypes.	Ranges not determinable in this way.

The Letter Classification worked in practice for two reasons. First, the sequences of faunas recognized by van der Vlerk and Umbgrove (1927) and by Leupold & van der Vlerk (1931) were broadly correct. Secondly, the stage assemblages were defined quite unambiguously in terms of larger foraminifera. It was, therefore, quite clear what was meant by T*d* or Tf_3 in terms of the foraminiferal fauna, whereas it was not at all obvious how the equivalents of certain European stages could be recognized outside the type localities.

One disadvantage of the Letter Classification has been the size of its units. Although it has always been easy to determine faunas including *Biplanispira* and/or *Pellatispira* as T*b*, it is as difficult today as it was forty years ago to say whereabouts in T*b* such faunas are situated. A late T*b* fauna cannot readily be distinguished from an early T*b* fauna, and the same is true of the faunas of most of the other Letter Stages. This situation exists because few people have given detailed descriptions of faunas from thick sections or from sequences including stage boundaries. Leupold & van der Vlerk (1931) gave such information as was then available regarding the sedimentary sequences and the nature of the stage boundaries in the areas which they described, but this was not amplified later by other workers, nor was it reflected in subsequent range charts.

(*b*) *Difficulties of inter-regional correlation*

The main problems encountered in correlating strata in the Indo-Pacific region, Europe and America may be summarized as follows:

1. The larger foraminifera of the Tethyan, American and Indo-West Pacific regions, although broadly similar, are sufficiently different in detail to make direct comparisons difficult. For example, the Upper Eocene of the Indo-West Pacific is characterized by the presence of *Asterocyclina*, *Biplanispira*, *Discocylina*, *Nummulites*, *Pellatispira*, and *Spiroclypeus*, whereas strata of the same age in the Americas contain an abundance of *Asterocylina*, *Lepidocyclina*, and *Helicolepidina*. Of these, only *Asterocyclina* and *Nummulites* (represented by a single Upper Eocene species in the Americas) are common to the two regions. For commentaries on provincialism in larger foraminifera see Cole (1960), Adams (1967) and references therein.

2. Stratigraphers are not yet agreed upon the relative positions and importance of all the European stages, some of which contain few, if any, larger foraminifera.

3. The Tertiary succession in north-west Europe is very thin compared with that in the Far East. It was deposited in a series of disconnected or poorly connected basins, and as much time may be represented by diastems as by fossiliferous sediments. Many important stages, e.g. Aquitanian, are not fully developed in marine strata.

4. From about Middle Miocene times onwards, the shrinking Tethys, of which Europe formed the northern margin, was not in direct connection with the Indo-Pacific, and the faunas in the two areas developed differently (see Adams 1967).

The prerequisites for a successful correlation between the Letter Stages and the European and American stages can also be summarized. They are:—

1. A generally accepted planktonic zonal scheme, applicable with minor local modifications only, within the latitudinal belt 45°N.–45°S.

2. An agreed sequence of stages in Europe, adequately defined both in terms of rock units and faunas—particularly their planktonic faunas.

3. Determination of the ranges of the age-diagnostic larger foraminifera in the Indo-Pacific and their correlation with the planktonic zonal scheme.

(*c*) *The facies problem*

The distribution of large foraminifera is influenced by facies to the same extent as other marine invertebrates, and one reason for choosing limestone successions for this study was to minimize the effect of environmental changes as far as possible. Even so, it is well known that marine carbonates accumulate under a wide variety of conditions and any changes affect the faunal composition of the sediments. These effects should not be under-estimated.

There are at least four main types of carbonate environment in which larger foraminifera occur:

1. Open-shelf. All depths down to the local base of the photic zone, a limiting factor for symbiotic algae which exist in the cytoplasm of some living foraminifera and for the calcareous algae which make up a considerable part of most Tertiary limestones.

2. Reefs. These faunas are rather specialized, and when *in situ* are readily

recognizable for obvious reasons. Recent reefs typically yield *Marginopora, Calcarina,* and encrusting genera in considerable abundance. Few true Tertiary reef faunas have been described.

3. Fore-reef shoals. Such deposits form extensively on the continental shelves and occupy a very narrow zone round the sides of atolls.

4. Back-reef environments (lagoonal). Shallow, sheltered water in an atoll or behind fringing or barrier reefs.

It is probable that most so-called fore-reef and back-reef assemblages (Pacific Isles excepted) are nothing more than accumulations of shells under typical open-shelf conditions, the fore-reef assemblages representing rougher and deeper water than those of the back-reef. There are no clear-cut distinctions between the different kinds of assemblage which tend to grade laterally into one another. Reef, littoral, and shoal faunas can become mixed by penecontemporaneous reworking—usually the movement of empty shells down the shelf or reef slope into deeper water. Larger foraminifera are sometimes found mixed with planktonics in the fine-grained basinal facies, and there are all gradations from fore-reef shoal to basinal deposits (Henson 1950). Larger foraminifera are also found in some deep-water carbonate turbidites, e.g., the Selidong Limestone, Sarawak (Adams & Wilford; in press), but here, despite their large numbers, they are very obviously redeposited.

The difficulties of correlating and dating different kinds of Cretaceous and Tertiary sediments in the Middle East have been highlighted by the work of Henson (1950) and van Bellen (1956). These authors were concerned with interdigitating open shoal, fore-reef, reef, and back-reef faunas. This problem has so far been less acute in the Far East where reef and back-reef faunas are less well known.

The genera and species shown on the range chart (Figure 3) as characterizing the various Letter Stages represent a variety of environments and are never all found together. For example, in Tertiary *a* it is common to find limestone assemblages made up largely of *Nummulites* and *Discocylina* while others consist exclusively of *Fasciolites, Orbitolites* and miliolids. The composition of these assemblages is controlled by environmental factors—in this case almost certainly by water depth. It is generally believed that the *Nummulites/Discocyclina* assemblage represents somewhat deeper water than that containing *Fasciolites* and *Orbitolites*. As might be expected, the two assemblages grade into one another.

In Tertiary *d* and *e*, the *Austrotrillina/Borelis/Peneroplis* assemblage invariably marks back-reef conditions while the *Heterostegina/Lepidocyclina* (*Eulepidina*) assemblage is more characteristic of open water, fore-reef environments.

In Recent seas, *Alveolinella, Marginopora* and *Sorites* are typical of shallow water (littoral and/or reef flats) whereas assemblages containing an abundance of *Cycloclypeus* indicate much deeper water. Examples could be multiplied, but these few suffice to demonstrate the importance of environment and facies.

The faunas mentioned above are all well known, and their stratigraphical and ecological significance is understood. But there is a danger that some fossils currently regarded as good stratigraphical markers may, in fact, be hitherto unrecognized facies fossils. Cole (1963) quoted Schlanger's unpublished suggestion that *Heterostegina borneensis* is such a fossil and that its occurrence in the Maemong

Limestone (T*e*) of Guam is without much stratigraphical significance. Schlanger argued that the *Heterostegina/Lepidocyclina* assemblage was characteristic of a fore-reef environment whilst *Miogypsinoides* and *Miogypsina* indicated shallow water, near-reef conditions. This hypothesis, as Cole showed, was hardly tenable even on the evidence from Guam and Saipan where good stratigraphical sections are lacking; it is firmly contradicted by the successions in Borneo (e.g. Melinau Limestone) where *H. borneensis* appears well before *Miogypsinoides* and *Miogypsina*, and where facies changes cannot be invoked as an explanation. This does not mean that Schlanger's idea was wholly wrong. Indeed, it seems probable that during the limited period of their co-existence the T*e* *Heterostegina/Lepidocyclina* and *Miogypsinoides/Miogypsina* assemblages had a similar relationship to that of *Discocyclina/Nummulites* and *Fasciolites/Orbitolites* in T*b*. Nevertheless, there can be no doubt that *H. borneensis* appeared well before *Miogypsinoides* and *Miogypsina*, and that their relationship was not simply one of mutual exclusion.

Although Cole (1963) did not accept Schlanger's suggestion that *H. borneensis* is a facies fossil and an unreliable marker for Lower T*e*, he subsequently suggested that difficulties in dating the middle part of the Bikini and Eniwetok successions could be accounted for by invoking facies (environmental) changes. He considers that the virtual absence of *Cycloclypeus* and the rarity of *Miogypsina* and *Lepidocyclina* in beds of T*f* age could indicate an environment " totally unfavourable for *Cycloclypeus* and not too favourable for the other two genera ". If this is so, it is necessary to explain the absence of markers such as *Alveolinella* and/or *Flosculinella* (depending on the age of the beds), peneroplids, *Marginopora*, etc. It is also necessary to ask why this part of the succession is so thin compared with the rest, if the whole of T*f*, T*g* and T*h* is represented.

Since the various kinds of carbonate sediments are not equally well developed in all parts of the Indo-Pacific region, it follows that knowledge of the assemblages characteristic of each environment is limited to those areas where the appropriate sediments occur. Reef and back-reef (lagoonal) facies seem to have been deposited less widely than the open shoal type, and it is predictable that the ranges of the individual genera and species which make up these assemblages will tend to lengthen as knowledge increases, while the ranges of those forms typical of the commoner types of limestones will remain fairly stable.

IV. REMARKS ON THE STRATIGRAPHICAL CHART AND RANGE CHART

(*a*) *The stratigraphical chart* (*Figure 2*)

This chart shows representative carbonate sequences containing larger foraminifera typical of the Letter Stages. Limestone successions have been illustrated because they are typically richer in larger foraminifera, are less affected by facies changes, and are generally better exposed than age-equivalent non-carbonate sediments. A few successions in argillaceous sediments, e.g. the Patala Shales of Pakistan, have been included because their faunas are better known than those of comparable limestones. Although these sections are believed to be the best described in the region at present, they are not necessarily the thickest or the most fossiliferous, and some future discoveries may well prove superior for purposes of regional correlation. Wherever

possible, sequences known to include stage boundaries have been selected. Some well-known and adequately described successions have been omitted because their inclusion would duplicate information already given without adding anything new. The relative geographical positions of the successions are shown on Figure 1.

Owing to the inadequacy of stratigraphical and palaeontological information at and near most of the stage boundaries, it is difficult to correlate strata exactly within a stage. Thus, it is not certain that the Nammal Shales (Ta_2) of Pakistan are the exact time equivalents of the Meting Limestone although they appear to be, or that the Tulki Limestone (Lower T*f*) of West Australia is precisely equivalent to the Bonya Limestone of Guam.

It is not intended that any of the successions shown here should be considered as type sections for the Letter Stages. They are, however, typical sections, i.e. places where faunas characteristic of the various stages have been found and described.

1. *The Dunghan Limestone*

The only description of this important succession which comprises 1,215 feet of Upper Cretaceous, Palaeocene and Lower Eocene beds at Dunghan Hill, is that of Davies (1941b). The samples on which Davies' brief account was based are deposited in the British Museum (Natural History), together with those from Mehrab Tangi where a 1,200 foot sequence of Upper Ranikot Limestone is said to occur.

2. *The Meting area*

The stratigraphy and larger foraminifera of the Laki Series were described by Nuttall (1925), and the thicknesses quoted here are those he gave for the succession three miles south of Meting. The foraminiferal faunas of the type Laki, about 190 miles N.N.E. of Meting, have never been described. Haque (1959) tried to show that the smaller foraminifera from the Meting Limestone indicated a Lutetian age, but Hottinger (in press) has recently dated the alveolines as Ilerdian.

3. *The Punjab Salt Range*

For details of the general succession and faunas see Nagappa (1959a and references therein). The unconformity shown on Figure 2 is deducible from the faunal change that occurs at the top of the Patala Shales (see Davies & Pinfold 1937). It is worth noting that Nagappa, Davies & Pinfold, and Haque (1956) all disagree about the thicknesses of the various lithological units from the Dhak Pass Beds upwards. Davies and Pinfold illustrate an unconformity between the Patala Shales and the Nammal Shales, whereas Haque shows the succession as continuous and conformable. McGowran (1968) pointed out that Haque's paper proves that a large part of the Nammal Shales must be Palaeocene in age. However, the implications of this are so important for regional stratigraphy that the section should be looked at again, and the anomalies explained, before it is used as a basis for any major correlation.

4. *The Khirthar Range*

The general succession was described by Vredenburg (1909) and the foraminiferal fauna of the Khirthar Series by Nuttall (1926 c & d). See pp. 102–103.

5. *The Kohat area*

The information for this sequence is taken from Eames (1952) and Nagappa (1959a).

6. *The Siju Limestone, Assam*

A general description of the Tertiary sequence and faunas of Assam may be found in Nagappa (1959a). Only the Siju Limestone, described by Ghosh (1954) and Samanta (1963) is shown here, as this part of the succession was once thought to be critical for the T*a*/T*b* boundary. It is now known to fall entirely within T*a* (Samanta 1968a).

7. *The Melinau Limestone, Sarawak*

This is one of the most complete mid-Tertiary carbonate successions yet to be described from the Far East (Adams 1965). The following additional information on the sequence was obtained as a result of a field study made in 1966.

a. *Biplanispira*, a genus not reported in 1965, has been found at a very high level in the T*b* part of the Melinau Gorge succession. This means that about 200 feet of limestone between T*b* and T*c* is devoid of age-diagnostic fossils, not 300 feet as stated previously.

b. *Spiroclypeus vermicularis* does not appear until about half way through the T*b* succession.

c. A disconformity, visible in the field, occurs between T*c* and T*d*. This accounts for the relative thinness of T*d*, the lower part of which is missing.

d. In 1965 it was stated that *Miogypsinoides complanatus* occurred throughout Lower T*e*. However, the records on which this range was based have since been checked and found to be erroneous. This species is, in fact, unknown from Melinau.

e. Random sections of the topmost beds of the limestone exposed in the Terikan River show a planktonic fauna including *Globigerinoides* cf. *quadrilobatus trilobus*, *G. sicanus* and *G.* cf. *altispira*, an indication that they probably belong to Bolli's *insueta* Zone (early part of Blow's Zone N8) and are somewhat younger than was thought previously.

f. *Heterostegina borneensis* van der Vlerk appears well below the first occurrence of *Miogypsinoides* (M. cf. *bantamensis*) and *Spiroclypeus*. This has been confirmed by careful collecting at close intervals in the Melinau Gorge.

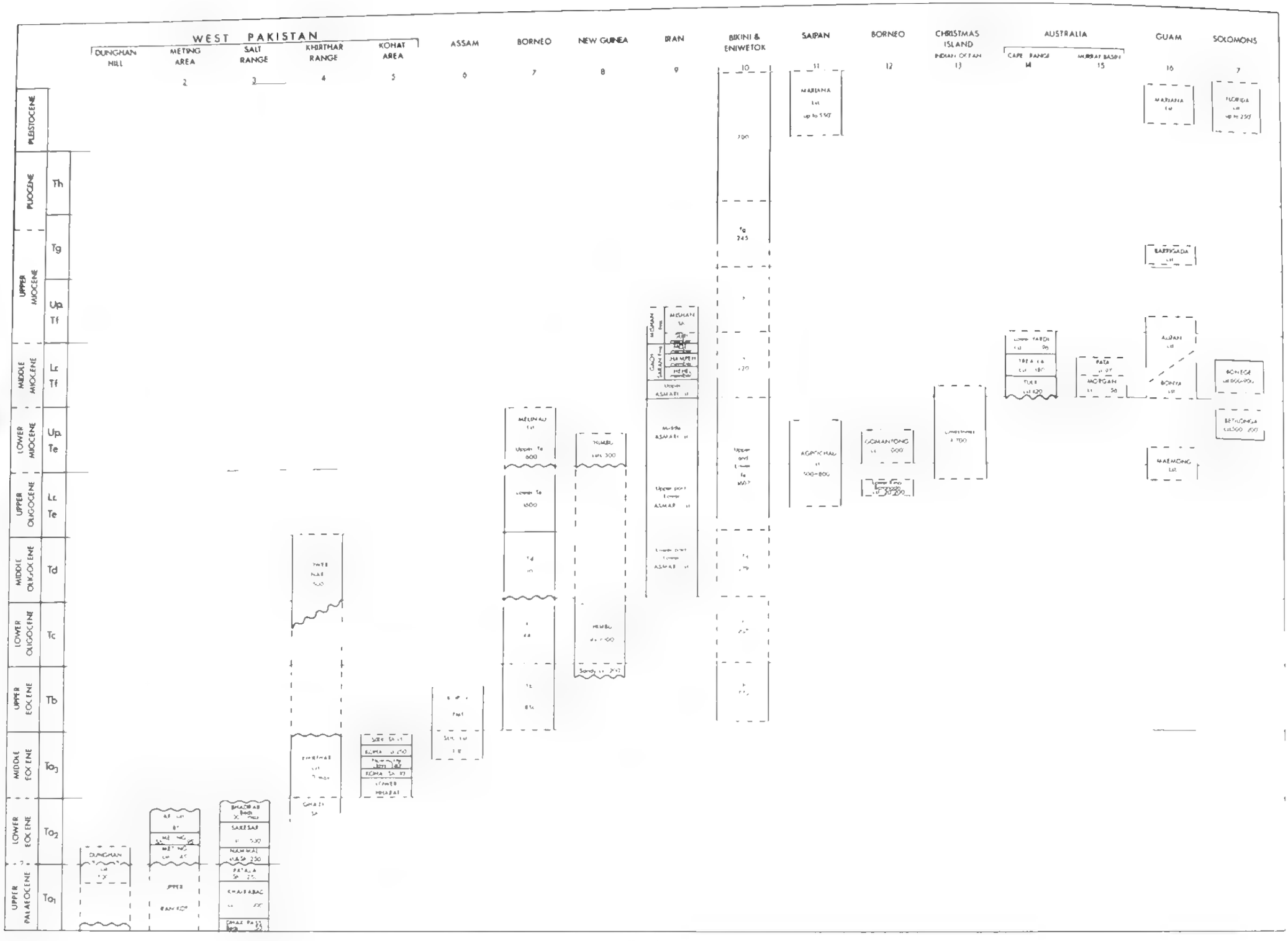
8. *The Chimbu limestones, New Guinea*

The general succession was described, and the fauna listed but not figured, by Rickwood (1955). These limestones are interesting because they comprise a considerable thickness of Tertiary *c* with subordinate Upper T*e* beds above. A detailed study of closely spaced samples from this succession would be well worth while. Some of Rickwood's foraminiferal determinations are certainly incorrect.

Present evidence suggests that in Papua at least, Lower T*e* faunas are poorly represented.

9. *The Asmari and Gach Saran Formations, Iran*

Important descriptions of the Asmari Limestone have been given by Thomas


WEST PAKISTAN
DUNGHAN HILL
METING AREA
SALT RANGE
KHIRTHAR RANGE
KOHAT AREA
ASSAM
BORNEO
NEW GUINEA
IRAN
BIKINI & ENIWETOK
SAIPAN
BORNEO
CHRISTMAS ISLAND
INDIAN OCEAN
AUSTRALIA
CAPE RANGE
MURRAY BASIN
GUAM
SOLOMONS
1
2
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PLEISTOCENE
PLIOCENE
UPPER MIOCENE
MIDDLE MIOCENE
LOWER MIOCENE
UPPER OLIGOCENE
MIDDLE OLIGOCENE
LOWER OLIGOCENE
UPPER EOCENE
MIDDLE EOCENE
LOWER EOCENE
UPPER PALAEOCENE
Th
Tg
Up Tf
Lc Tf
Up Te
Lc Te
Td
Tc
Tb
To3
To2
To1

FIG 2

(1950), Kent, Slinger & Thomas (1951), Eames *et al.* (1962) and James & Wynd (1965). Thomas reported, but did not figure or describe, *Cycloclypeus* and *Spiroclypeus* from surface outcrops (Tangi-i-Gurguda) at the base of the limestone. These records have never been confirmed although they were repeated by James & Wynd. If correct, they would have an important effect on mid-Tertiary correlation in the area.

James & Wynd listed (p. 223) the following foraminifera from the Champeh and Mol Members of the Gach Saran Formation: *Borelis melo, Flosculinella, Miogypsina, Peneroplis farsensis* and *Taberina malabarica*; and *Flosculinella* cf. *bontangensis* from 480 feet above the base of the laterally equivalent Rajak Formation. *F. bontangensis, Borelis melo, Operculina complanata* Defrance, *Nephrolepidina, Taberina malabarica* were listed from the base of the overlying Mishan Formation (Guri Limestone Member). Only *Miogypsina* sp., *Nephrolepidina* sp. and *Operculina complanata* were figured. These assemblages are characteristic of Lower T*f* and, if the species are correctly identified, prove a direct sea connection with the Indian Ocean.

10. *Bikini and Eniwetok atolls*

A composite section compiled from the data provided by Cole (1954, 1958), Todd & Post (1954) and Todd & Low (1960) is illustrated here. The maximum thickness quoted for each Letter Stage in the drill holes on the two atolls has been used.

As Cole himself observed, it is questionable whether T*c*/*d* beds are really represented in these holes. No diagnostic fossils have been found and the dating rests purely on negative evidence. Tertiary *b* is well represented in the Eniwetok bores but was not penetrated on Bikini.

Tertiary *e* is present in the cores from both atolls, and at Bikini both Upper and Lower divisions were recognized by Cole. Tertiary *f* is a problem. Cole assigned a maximum of 350 feet of limestone to this division, basing his dating on the occurrence of *Cycloclypeus indopacificus vandervlerki* and *Lepidocyclina orientalis* in Eniwetok, and on the latter species only in Bikini. However, no absolutely diagnostic Upper T*f* species were found. Adams (1968) noted that the specimens referred by Cole (1954 : 258) and by Todd *et al.* (1954, 1960) to *Austrotrillina howchini* should really have been assigned to *A. striata*, a T*e* species, and it now seems very probable that Tertiary *f*, if it occurs at all, is represented only by the lowest levels of Lower T*f*, and that a disconformity separates the oldest Miocene horizons from the overlying Pliocene. No diagnostic Middle or Upper Miocene planktonic species were reported from these drill holes.

11. *Saipan*

The geology and larger foraminifera were first described by Cole & Bridges (1953), further extensive accounts being given by Cole (1957) and Hanzawa (1957). Unfor-

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FIG. 2. Representative sections through described successions, mainly carbonates, ranging in age from Palaeocene to Recent. For details see pp. 94–99. Precise correlation of all the limestone units within each Letter Stage is not at present possible. The correlation between the Letter Stages and the Epoch/Sub-Epoch names for the Cainozoic reflects the writer's current opinion and is only to be regarded as approximate.

tunately, owing to the nature of the terrain, the samples on which these accounts were based were not collected in any known stratigraphical order, and the results have to be interpreted in the light of knowledge derived from better exposed successions elsewhere. The smaller foraminifera of the island were described by Todd (1957).

12. *The Kinabatangan and Gomantong limestones, Sabah*

The numerous small Upper and Lower T*e* limestones along the lower course of the Kinabatangan River in Sabah, Borneo, along with the much larger Gomantong Limestone, have been studied by the writer and the results are now being prepared for publication. They confirm the faunal sequence described from the Melinau Limestone, Sarawak.

13. *Christmas Island (Indian Ocean)*

The so-called Miocene orbitoidal limestones were first described by Jones & Chapman (1900). Nuttall (1926a) revised the Orbitoids, and Ludbrook (1965) described the fauna from a few additional samples. The whole of the post-Eocene limestone succession has recently been carefully resampled along several traverses by D. J. Belford who, together with the writer, is preparing a description of the faunal succession. It is sufficient to state here that the lower part of the limestone (approximately 250 feet) is Lower T*e* in age, whilst the rest, apart from the uppermost 50 feet or so, is Upper T*e*. The highest beds can be dated as Lower T*f* on the presence of *Flosculinella bontangensis*. It is interesting to note that such well-known " species " as *Eulepidina ephippioides* and *E. andrewsiana*, for both of which Christmas Island is the type locality, come from the lower part of T*e*.

14. *The Cape Range limestones, Western Australia*

This sequence includes four limestones, all of which were described by Crespin (1955). The Trealla and Tulki limestones contain good Lower T*f* faunas but the underlying Mandu Limestone is more difficult to date. The type section for the Mandu Limestone contains a fauna which suggests a Lower T*e* age, but additional species listed by Crespin from nearby localities indicate that the age is more probably Upper T*e*. In view of this uncertainty, the Mandu Limestone is omitted from the chart. There is, in any case, a disconformity between the Mandu (T*e*) and Tulki (T*f*) limestones as was recognized by Crespin.

15. *The Morgan and Pata limestones, Murray Basin, South Australia*

The stratigraphy and fauna of the limestones in the Murray Basin were described by Ludbrook (1961). The Pata Limestone is important in the present context because it contains *Austrotrillina howchini* in association with *Orbulina universa*. The thicknesses shown in Figure 2 are for the type sections of the Morgan Limestone (including the Cadell Marl Lens) and for the standard subsurface section of the Pata Limestone.

16. *Guam*

The stratigraphical succession and faunas were described by Cole (1939, 1963) and Todd (1966). Unfortunately, the samples from which the micro-faunas were described could not be collected in stratigraphical order, and in places the sequence is not very well understood.

The youngest carbonate on the island, the Mariana Limestone, was assigned to the Pleistocene by Cole and by Todd. It contains *Baculogypsina sphaerulata, Calcarina spengleri, Cycloclypeus carpenteri, Heterostegina suborbicularis*, and *Marginopora vertebralis*. Similar faunas occur at the same level in Saipan.

The Barrigada Limestone contains *Cycloclypeus postindopacificus, Operculina lucidisutura* and *O. rectilata*, and was dated as Tg by Cole. In this paper *C. postindopacificus* is not distinguished from *C. carpenteri*. Cole's age determination depended on the presence of *O. lucidisutura* and *O. rectilata*, species which he had previously reported from Bikini and Eniwetok.

Strata mapped as part of the Alifan Limestone contain *C. carpenteri, M. vertebralis, Heterostegina suborbicularis* and, at lower levels, *Miogypsinoides cupulaeformis* and *Rotalia atjehensis*. Cole's suggestion that the lower horizons can be correlated with the Bonya Limestone is reasonable.

The Bonya Limestone contains cycloclypeids which have been referred to *C.* (*K.*) *annulatus, C. indopacificus* and *C. posteidae*, together with *Flosculinella bontangensis, Nephrolepidina japonica, N. rutteni* and *Marginopora vertebralis*, an assemblage clearly denoting a Lower T*f* age. *Miogypsinoides cupulaeformis* and *Nephrolepidina sumatrensis* are also present. This appears to be the only well-documented record of *Miogypsinoides* in strata of Lower T*f* age.

The Maemong Limestone is divisible into two parts : an upper portion with *C. eidae, Eulepidina ephippioides, Spiroclypeus higginsi, Miogypsinoides dehaarti, N. sumatrensis*, and *N. verbeeki* (an assemblage indicative of Upper T*e*), and a lower portion with *Heterostegina borneensis, Eulepidina ephippioides, Miogypsinoides bantamensis, Nephrolepidina sumatrensis* and *Spiroclypeus yabei* (an assemblage indicative of late Lower T*e*).

17. *Succession in the Solomon Islands*

Coleman (1963) described the stratigraphy and foraminiferal faunas of these islands. A few of the limestones are shown on Figure 2 ; the remainder only repeat the faunas found in successions elsewhere in the region and are not included.

(b) *The Range Chart* (*Figure 3*)

The genera and species shown on this chart are those for which the most reliable stratigraphical data are available. Many species of potential stratigraphical importance have been omitted because their ranges cannot be determined at present or because they have so far been described from one locality only. Some important species are known only from isolated samples, e.g. *Lacazinella wichmanni*. These are included only when they can be dated accurately from the associated fauna.

The ranges shown on this chart can be checked by reference to the carbonate

sequences shown in Figure 2, or, in the case of species like *L. wichmanni*, by reference to the relevant notes in the text.

Solid lines indicate that ranges are well established and verifiable, usually by reference to one or more of the successions shown in Figure 2 ; broken lines indicate a degree of uncertainty. Thus, *Heterostegina borneensis* is represented by a solid line throughout the upper part of Lower T*e* where it can be proved to occur, and by a broken line through the lower part of this division where proof is lacking although records exist. Species represented only by broken lines have not, of course, been described from any of the successions shown on Figure 2.

Although this paper is based primarily on larger foraminifera, certain smaller benthic and pelagic genera (e.g., *Austrotrillina, Halkyardia* and *Orbulina*) are included as they are readily determinable in random sections of limestone.

V. NOTES ON THE STAGES AND STAGE BOUNDARIES

Very few adequately described sequences include stage boundaries, and there are even fewer in which sedimentation can be shown to have been continuous from one stage to another. Stage boundaries will, of course, always be difficult to locate accurately in sections where sedimentation was uninterrupted, as in such places faunal changes are likely to be gradual rather than abrupt. In the absence of facies changes, sudden faunal alterations normally suggest discontinuities (diastems) whether or not these can be recognized in the field. Catastrophic events could produce similar effects, but such phenomena are rare.

Throughout this section, each Letter Stage is first defined in terms of genera and species which are restricted (or almost restricted) to it, or which are especially prominent in the fauna. The faunal diagnosis is followed by comments on the best known sections and localities, and on areas which may in future prove to include good examples of the stage faunas.

Tertiary a_1 (late Palaeocene)

Diagnostic fauna : *Actinosiphon punjabensis, Assilina dandotica, Discocyclina ranikotensis, Fasciolites* (including *F. vredenburgi*), *F.* (*Glomalveolina*), *Lockhartia* spp., *Miscellanea miscella, Nummulites nuttalli, N.* spp., *Operculina sindensis, O. canalifera, Saudia labyrinthica.*

This fauna is virtually restricted to the Palaeocene. There are very few records of larger foraminifera from definite " Lower " and " Middle " Palaeocene sediments anywhere in the world, a reflection partly of the fact that beds of this age are rarely developed in the right facies for larger foraminifera and partly of a confusion in terminology. The introduction of the Ilerdian stage in 1960 changed the whole concept of Palaeocene for some workers.

No Ta_1 sections have been described from south-east Asia although faunal assemblages of this age are known (see Liechti *et al.* 1960 and Adams 1965). Van der Vlerk & Umbgrove (1927) reported *N. nuttalli, N. kelatensis,* and *N. thalicus* from Borneo, but these typical Palaeocene species were thought by later authors to occur at the same level as *Pellatispira,* and their stratigraphical significance was thus obscured.

The best Palaeocene sections are in West Pakistan where the so-called " Ranikot

fauna " includes most of the genera and species listed above. According to Pascoe (1963 : 1477) the Ranikot Series in Sind " is divisible into a lower fluviatile stage, usually from 1,000–1,200 feet thick but reaching a maximum of 1,500 feet, and an upper marine stage usually 700–800 feet thick but rising to a maximum of about 1,000 feet ". The Ranikot fauna has not been described from the type section (Rani-jo-kot, Sind) in the northern part of the Laki Range where, according to Williams (1959), the beds are thick, non-marine and unfossiliferous except for plant remains, but from farther south (Nuttall 1926b) and from Thal over 500 miles to the north (Davies 1927).

The Ta_1/Ta_2 boundary

No continuous carbonate succession across this boundary has been described, and so far as is known there is a faunal break between the youngest Ta_1 and oldest Ta_2 larger foraminiferal assemblages everywhere in the region. In West Pakistan there are certainly localities where strata of Ta_2 age rest on beds of Ta_1 age (e.g., Dungan Hill and Mehrab Tangi, Baluchistan, and at Thal, N.W. Frontier Province (Davies 1927)). The Dunghan Limestone includes beds of Upper Cretaceous, Palaeocene and Lower Eocene age (Davies 1941b), but the faunal sequences are either undescribed or need describing in more detail.

Tertiary a_2

DIAGNOSTIC FAUNA : *Assilina* (including *A. leymerie* and *A. granulosa*), *Discocyclina*, *Fasciolites* (including *F. globosa*, *F. oblonga* and *F. subpyrenaica*), *Nummulites* spp. (including *N. atacicus*), *Opertorbitolites douvillei*, *Orbitolites complanatus*, *Somalina*.

In the Laki Range (West Pakistan) the fossiliferous Ta_2 comprises the Laki limestone (200 feet) and the underlying Meting Shale (320 feet). These are generally believed to be equivalent to the Ghazij Shales (1,960 feet thick in the type section at Spintangi, but elsewhere varying in thickness from 700 to almost 8,000 feet according to Williams (1959). The lowest beds of the Ghazij Formation may in places be Palaeocene in age but the greater part is said to be Lower Eocene. This formation is believed to be overlain conformably by the Khirthar Formation. The foraminiferal faunas from the best sections (Laki Range, Sulaiman Range etc.) are either undescribed or need describing in greater detail than has been possible hitherto. The Laki, Meting, Sakesar limestones and their equivalents have traditionally been regarded as Lower Eocene in age but this is increasingly being questioned. Haque (1956) showed that the typical Ta_2 larger foraminifera of the Nammal Shales first occur well below the last occurrence of *Globorotalia velascoensis* and other supposedly good Palaeocene markers in the Nammal Gorge. Hottinger (in press) has identified several species of typical Ilerdian alveolines from the Meting Limestone. If the Ilerdian is accepted as being entirely Palaeocene in age, then there is no doubt that the Palaeocene/Eocene boundary in Pakistan will have to be raised considerably. Most of Ta_2 will then be assigned to the Palaeocene. However, the writer thinks it best to defer judgement on this issue until the faunas of the area have been redescribed, and Hottinger's zonal scheme has been properly tested in the Far East.

No Ta_2 carbonate sequences with larger foraminifera have yet been described from

south-east Asia or the Pacific Isles, and it is possible that this division is missing over large parts of this area. Doornink's record (1932) of Lower Eocene faunas from Java is incorrect. The beds concerned contain *Pellatispira*, a characteristic Upper Eocene genus.

The Ta_2/Ta_3 (Lower/Middle Eocene) boundary

The only described sections are in West Pakistan, but even here much detailed work remains to be done. If the faunal changes are as abrupt as the published evidence suggests (Nuttall 1926*d* ; Davies 1927, 1940b ; Nagappa 1959), then this boundary is probably a disconformity almost everywhere. The sudden faunal change could, on the other hand, simply reflect our inadequate knowledge of faunas immediately adjacent to the boundary.

Tertiary a_3 (Middle Eocene)

DIAGNOSTIC FAUNA : *Assilina* (including *A. spira, A. exponens, A. cancellata*), *Asterocyclina, Dictyoconoides cooki, Discocyclina* (including *D. sowerbyi, D. javana, D. dispansa*), *Fasciolites* (including *F. elliptica, F. wichmanni*), *Nummulites* (including *N. atacicus, N. carteri, N. gizehensis, N. javanus, N. perforatus, N. millecaput*), *Orbitolites complanatus, Somalina.*

No Ta_3 section has yet been described from south-east Asia or the Pacific Isles, although isolated faunas of this age are known from Java (Doornink 1932), Timor (Henrici 1934) and New Guinea (Rutten 1936).

It has often been assumed that the very large species of *Nummulites* (*N. carteri, N. javanus, N. gizehensis, N. millecaput* etc.) are restricted to the Middle Eocene, but this has never been shown to be true for the whole area. Although Samanta's (1965) Upper Eocene dating for the upper part of the Siju Limestone, which contains *N. gizehensis* and *N. perforatus*, was subsequently changed to Middle Eocene (Samanta 1968a), there is still a possibility that some large nummulites range up into the early part of T*b* (e.g., *N. javanus* in Borneo. Adams 1965). Some range charts suggest that the large nummulites all appeared together at the base of the Middle Eocene and became extinct simultaneously at the top, but this is highly improbable.

The Khirthar Formation in its type section (Gaj River) ranges from Middle Eocene to Lower Oligocene (Williams 1959, Khan 1967). Nuttall's descriptions (1926c & d) of the Middle Khirthar faunas were not based on continuous sampling but on isolated samples collected over a large area during a reconnaissance survey of parts of western India in 1920–21. The ranges he quotes for the larger foraminifera are, therefore, very inexact.

The Ta_3/T*b* (Middle/Upper Eocene) boundary

No described Indo-Pacific carbonate succession is known to be continuous across this boundary.

Ghosh (1954) described what he thought was the Middle/Upper Eocene boundary from the Siju Limestone in Assam, and Samanta (1962 & 1963) described the foraminiferal fauna. He, like Ghosh, assigned the lowermost 82 feet to the Middle Eocene and the uppermost 240 feet to the Upper Eocene. However, he subsequently

decided (1968a) that the specimens of *Pellatispira* on which the Upper Eocene determination mainly rested, were not true representatives of the genus. He, therefore, provisionally assigned the upper part of the limestone to the Middle Eocene, observing that its faunas could be regarded as transitional between Middle and Upper Eocene.

The limestone succession in the Khirthar Range (West Pakistan) is in need of careful study. Williams (1959) stated that the Upper Eocene in this area is developed in pelagic facies, but he did not mention the nature of its junctions with the Middle Eocene and Oligocene. Khan (1967), on the other hand, dated these beds with pelagic foraminifera as Middle Eocene.

Schweighauser (1953) described the faunas across the Lutetian/Priabonian boundary in northern Italy. Here, as in Somalia according to the work of Azzaroli (1952), the overlap of the age-diagnostic marker genera makes the exact position of the boundary a matter of opinion.

Tertiary *b* (Upper Eocene)

DIAGNOSTIC FAUNA : *Asterocyclina* (including *A. matanzensis* Cole), *Biplanispira*, *Discocylina* (numerous species including *D. omphalus*, *D. dispansa*, *D. sella*) *Lacazinella wichmanni*, *Nummulites fabianii*, *N. pengaronensis*, *N. chavennesi*, *Pellatispira*, *Spiroclypeus albapustula*, *S. vermicularis* and *Wilfordia sarawakensis*.

This stage is very well represented throughout the whole of south-east Asia and the Pacific, and its microfaunas are currently better known than those of any other part of the Palaeogene. Tertiary *b* larger foraminifera are not, however, well represented in carbonate sediments on the Indian sub-continent. The best-known sequences are in Borneo (Adams 1965), Saipan (Cole 1957, Hanzawa 1957), Somalia (Azzaroli 1952) and in the Pacific Isles (Cole 1954, 1958). Many authors have described faunas from isolated samples in different parts of the region (e.g., Java, Doornink 1932 ; Pakistan, Eames 1952 ; India, Samanta 1965) but despite this, the faunal sequence has not been properly established and the potentialities of the larger foraminifera for zoning the Upper Eocene have by no means been fully exploited. We do not know the exact range of a single species of *Pellatispira*, *Biplanispira*, *Discocylina*, or for that matter of any species of *Nummulites*. This simply reflects a general failure on the part of authors to describe sections in detail, and can certainly be corrected in the future.

The T*b*/T*c* (Eocene/Oligocene) boundary

The only known sections across this boundary are in the gorges of the Melinau and Medalam rivers in north-east Sarawak, Borneo. These two sections are five miles apart, and in both the boundary is hard to place because the faunal change is gradual (Adams 1965 and paper in preparation). As stated earlier, the Khirthar Formation in its type locality is known to range from Middle Eocene to Lower Oligocene (Williams 1959 : 390). All previous authors (also Pascoe 1963) state that there is a substantial break between the Khirthar and the Lower Nari, all the Upper Eocene being missing. Khan (1967) has shown that in the Badhra area of Sind there is a marked disconformity between the Middle Eocene and the Middle Oligocene,

at the base of which there is a limestone conglomerate. He claims that in the Gaj River succession, Lutetian-basal Auversian faunas of pelagic and benthic foraminifera (presumably those described as Upper Eocene by Williams 1959) are followed by Lower Oligocene (Lattorfian) larger foraminifera.

Tertiary *c* (Lower Oligocene)

DIAGNOSTIC FAUNA : *Nummulites* (particularly *N. fichteli*) without *Eulepidina. Borelis, Cycloclypeus koolhoveni, Dictyoconus melinauensis, Heterostegina bantamensis, H. praecursor, Lacazinella reicheli, Nummulites vascus, N. pengaronensis, N. fichteli, Praerhapydionina delicata.*

Although T*c* faunas are known to be widespread, few sequences through rocks of this age have been described. The thickest succession so far found is in the Melinau limestone, Sarawak (more than 1,000 feet). The thinner Sarang limestone, also in Sarawak, is entirely of T*c* age (Adams 1964). Tertiary *c* limestones occur in New Guinea, and in the Chim Gorge (West Central Highlands, Papua) at least a thousand feet of limestone contains *N. fichteli, Heterostegina, Operculina,* etc. (A.P.C. 1961). Faunas of this age are known from the Moluccas (Bursch 1947) and from many localities in Indonesia (see van Bemmelen 1949), but described successions are lacking.

The lower part of the Nari Formation in Pakistan (about 1,500 feet thick according to Pascoe 1963 : 1618), although mainly Middle Oligocene in age, is said to be conformable with the Khirthar Formation except at the southern end of the Khirthar Range (Williams 1959) and must, therefore, include beds of Lower Oligocene age. Williams proposed that the type section should be taken as the Gaj River, presumably because the succession there is better exposed and more accessible than in the area originally mentioned by Blanford* (1879), the Nari Nai, a river a few miles to the south. Several authors (e.g., Nuttall 1925) have described reticulate nummulites from the Nari beds, but no one has described the entire foraminiferal fauna or has examined samples collected in stratigraphical order through continuous sections. Most of the Lower Nari is of Middle Oligocene age, and in places where *Lepidocyclina* appears at the base the entire thickness must locally be assigned to the Middle Oligocene.

The T*c*/T*d* (Lower/Middle Oligocene) boundary

The only place where this boundary has been observed in the field is the Melinau Gorge, Sarawak. The junction there is a clearly marked erosion surface (personal observation 1966) and there is a sudden faunal change as the boundary is crossed (Adams 1965).

Tertiary *d* (Middle Oligocene)

DIAGNOSTIC FAUNA : *Nummulites* (mainly reticulate forms, *N. fichteli*) and *Lepidocyclina* (*Eulepidina*) spp., *Borelis* (including *B. pygmaeus*), *Cycloclypeus oppenoorthi* (and, perhaps, transitional forms to *C. eidae*), *Heterostegina* spp.

* See Medlicott & Blanford (1879).

Faunas of this age are known from East Africa (Azzaroli 1958), Iraq, Iran (Eames *et al.* 1962), West Pakistan, Borneo, New Guinea and elsewhere. However, with the possible exception of the Lower Nari Beds, no thick successions have been reported.

Only the upper part of T*d* is present in the Melinau limestone (Sarawak), and the most likely places for the lower part to be found seem to be in Pakistan (Lower Nari Formation) and New Guinea (New Guinea Limestone).

Tertiary *d* is defined by the association of *Nummulites* and *Eulepidina*. It seems probable that *Eulepidina* and *Nephrolepidina* appeared simultaneously in the Far East and if this can be confirmed, the association of *Nummulites* and *Lepidocyclina s.l.* (excluding any Eocene species) will be sufficient to identify T*d*.

The T*c*/T*d* boundary, being defined on the first appearance of *Eulepidina*, is almost certainly diachronous. Since *Nummulites* and *Eulepidina* do not always occur in association, it is probable that some isolated occurrences of T*d* rocks containing only *Nummulites* have been recorded as T*c*, while others containing only *Eulepidina* have been dated as T*e*.

The T*d*/T*e* (Middle/Upper Oligocene) boundary

The best known section is in the Melinau Gorge, Sarawak, where the faunal change is gradual and deposition was continuous between the two stages. This boundary was first described by the author (1965) and a further description based on additional material is now in preparation.

The only sections which Leupold and van der Vlerk (1931) thought were continuous across the T*d*/T*e* boundary were:—

a. In the north-central Boraoe (Kalimantan) where they reported :

Globigerina mergels	T*e*
Lepidocyclina kalk	T*d*
Seilor-lagen	T*c*

but the fauna from the critical part (T*d*/T*e*) of this succession was neither described nor listed.

b. In the Tidoengsche Landen (Kalimantan), *Nummulites fichteli* is said to occur in association with *Eulepidina* in the Tempilan beds (1000 metres thick), *Heterostegina* is said (p. 626) to be represented by *H. ruida* in these beds, and not by *H. borneensis* which occurs in the overlying Mesaloi marls (also about 1000 metres thick). There is, however, no published description of this faunal sequence nor of any lithological change that may occur at the boundary.

It is evident that if T*d* is synonymous with Middle Oligocene the Oligo/Miocene boundary must fall somewhere within T*e*, probably fairly near the top. There appears to be little evidence to support the widely held belief that *Miogypsinoides* and *Spiroclypeus* range down to the base of T*e*. Such evidence as exists (mainly from Sarawak) suggests that they appear fairly late in Lower T*e*, i.e. above the first appearance of *H. borneensis*.

Lower Tertiary *e* (= Te_1/Te_4)

DIAGNOSTIC FAUNA : *Austrotrillina striata, A. asmariensis, Cycloclypeus eidae, Heterostegina borneensis, Lepidocyclina* (*Eulepidina*) spp., *L.* (*Nephrolepidina*) *isolepidinoides, N. parva* (other species at high levels), *Miogypsinoides complanatus, M. bantamensis, Spiroclypeus* spp.

This stage is well developed over the whole area, the best faunas being known from Borneo (Adams 1965), Saipan (Hanzawa 1957, Cole 1957), and the Pacific Isles (Cole 1954, 1958). For many years it has been customary to equate Lower T*e* with early Lower Miocene on the ground that the larger foraminiferal assemblages are the equivalents of the Aquitanian of Europe, but this correlation cannot be justified. The only larger foraminifera in the stratotype Aquitanian are miogypsinids and a primitive *Heterostegina* (Drooger *et al.* 1955), and the correlation therefore depends on plankton and on larger foraminifera found in other sections. It is probable that much of the Upper Nari of Pakistan (maximum thickness 5–6,000 feet ; Pascoe 1963 : 1617) is Lower T*e* in age. This formation is, however, largely unfossiliferous and passes gradually into the underlying Lower Nari (T*d*). See Pascoe (1963 : 1620).

The Lower/Upper T*e* (Oligocene/Miocene) boundary

This can be recognized over the whole of the western Pacific and throughout Indonesia. It appears to be peculiar to the Indo-Pacific Province and not to be recognizable with certainty elsewhere. In the writer's opinion, it corresponds approximately to the Oligocene-Miocene boundary in Europe. The best known sections for the study of this boundary are in Iran (Asmari Limestone), Christmas Island, Sarawak (Melinau Limestone) and New Guinea (Kereru Limestone). The New Guinea sections are believed to be well exposed but need to be re-collected and described in detail ; the Christmas Island sequence is good and is now being redescribed by the writer and Dr. D. J. Belford (Bureau of Mineral Resources, Canberra). In the Melinau limestone, Sarawak, the junction is almost certainly disconformable, but it has not yet been observed in the field.

Upper Tertiary *e* (= Te_5)

DIAGNOSTIC FAUNA : *Austrotrillina striata* grading into *A. howchini* at high levels, *Cycloclypeus eidae* group, *Flosculinella reicheli, F. globulosa, Lepidocyclina* (*Eulepidina*), *L.* (*Nephrolepidina*) *inflata, N. japonica, N. sumatrensis* in abundance, and *N. verbeeki, Miogypsina* spp. (including *M. thecideaeformis*), *Miogypsinoides dehaarti, Spiroclypeus* spp.

Rocks of this age are also well developed over the whole province. The best-known faunas are from Borneo, Saipan, New Guinea and the Pacific Isles. The highest T*e* beds in the Melinau Limestone have recently been found to contain a planktonic fauna (see p. 96) almost certainly referable to Banner & Blow's Zone N8 (late *insueta* Zone of Bolli). The Lower Rembang beds of Java are of Upper T*e* age (van der Vlerk 1928).

The Upper T*e*/Lower T*f* (Lower/Middle Miocene) boundary

The best section so far discovered is on Christmas Island (Indian Ocean) but there

the T*f* fauna is represented only by *Flosculinella bontangensis*. Better sections undoubtedly exist in New Guinea but they await description. In the Cape Range (Australia) the T*e*/T*f* boundary is a disconformity (Crespin 1955).

The deep drill holes on Bikini and Eniwetok atolls pass through the boundary but its recognition is difficult in the absence of continuously cored material.

Leupold and van der Vlerk (1931) showed the T*e*/T*f* boundary as occurring within the Tabellor limestones (thought to be about 600 metres thick) on the Mangkalihat Peninsula, Borneo, but the faunas from these beds have never been described and the evidence on which the boundary is based is unknown.

In Pakistan, the T*e*/T*f* boundary must fall somewhere within the Gaj beds which, in the type locality (Gaj River) are 1,500 feet thick (Pascoe 1963) [2,020 feet according to Williams (1959 : 390)]. The basal beds of the Gaj Formation are calcareous (limestones and shales) whereas the higher beds are mainly sandstones, shales and gypseous clays. According to Vredenburg (1906) the Gaj rocks of Sind are often crowded with *Lepidocyclina marginata* (Michelotti), a species often reported from strata of Oligocene and Lower Miocene age in Europe.

Lower Tertiary *f* (= Tf_1/Tf_2)

DIAGNOSTIC FAUNA : *Alveolinella fennemai auctt.* (probably merely a primitive form of *A. quoyi*), *Austrotrillina howchini*, *Borelis melo**, *B. melo curdica**, *Cycloclypeus posteidae*, *C. indopacificus*, *C.* (*Katacycloclypeus*) *annulatus*, *Flosculinella bontangensis*, *Lepidocyclina* (*Nephrolepidina*) spp. including *N. ferreroi*, *N. sumatrensis*, *N. martini*, *N. japonica*, *N. orientalis*, *Marginopora vertebralis*, *Miogypsina* spp., *Orbulina suturalis*, *O. universa*, *"Taberina" malabarica*.

Limestones of this age are widespread in the Indo-Pacific region but few faunal sequences have yet been properly described. Exceptions are the successions in the Solomon Islands described by Coleman (1963) and in the Cape Range, Australia (Tulki and Trealla limestones) described by Crespin (1955). New Guinea is a most promising area for future research. Cole (1963) dated the Bonya limestone of Guam as T*f*. The main part of its fauna is, however, consistent with a Lower T*f* age. The Upper Rembang beds of Java are also of this age (van der Vlerk 1928).

The Lower/Upper T*f* boundary

No good sections across this boundary are known to the writer. It may occur in the Alifan limestone of Guam and could in future be found in New Guinea.

Leupold and van der Vlerk (1931) regarded the Upper Balikpapan beds of Borneo as Tf_3 and the Lower Balikpapan beds as Tf_2. The total thickness of these beds was given as 1,200 metres, but much of this consists of barren sandstones and coal. The limestone faunas, on which the dating depends, occur at various unspecified levels near the top and base of the succession. No descriptions of the limestones or of the faunas have been published.

* Known from East Africa & the Middle East (Eames *et al.* 1962) but not with certainty from Indonesia and the Pacific.

Upper Tertiary *f* (= T*f*$_3$)

DIAGNOSTIC FAUNA : *Alveolinella quoyi, Cycloclypeus carpenteri/guembelianus, Heterostegina* spp., *Lepidocyclina rutteni* (probably restricted to the lower part), *L. radiata, Lepidocyclina orientalis, L. talahabensis, Marginopora vertebralis, Operculina* spp. (*Orbulina* is very common in Upper T*f* and younger limestones).

Although faunas of this age are well known, no carbonate successions of any great thickness have been found. Upper T*f* faunas might be expected in the Bikini and Eniwetok drill holes but typical assemblages seem to be lacking. The Tji Lanang and Njalindung beds of Java are usually assigned to Upper T*f*.

The T*f*/T*g* boundary

This does not appear to have been described from a carbonate sequence or, indeed, from any other succession in which it can be recognized on the basis of larger foraminifera. Cole (1963) thought that it might occur in the Alifan limestone of Guam but the evidence for this is very weak.

Tertiary *g*

DIAGNOSTIC FAUNA : *Alveolinella quoyi, Cycloclypeus carpenteri/guembelianus* and *C. postindopacificus, Operculinoides rectilata, O. lucidisutura.* The assemblage is similar to that of Upper T*f* but lacks *Lepidocyclina.* Tertiary *g* was originally defined as " young Miocene without orbitoids " by Leupold & van der Vlerk (1931).

The Barrigada limestone of Guam has been dated as T*g* by Cole (1963), who also thinks that parts of the sections in the Eniwetok and Bikini drill holes can be assigned to this stage. He may be right, but the evidence is very slender and is susceptible to more than one explanation.

Assemblages of T*g* larger foraminifera have not so far been recorded outside the Pacific Islands.

The T*g*/T*h* boundary

The only continuous carbonate sequences thought to include this boundary were described from the Bikini and Eniwetok drill holes (Cole 1954, 1958). Its position cannot, however, be recognized from the larger foraminifera which by this time had declined in variety and importance.

Tertiary *h*

DIAGNOSTIC FAUNA : as for T*g* with the addition of *Borelis schlumbergeri* and perhaps *B. pulchrus.* *

There are no well-described sections through strata assigned to this stage and the faunas are poorly known. Leupold & van der Vlerk (1931) regarded T*h* as equivalent to Pliocene but were unable to distinguish its faunas from those of T*g*.

In favourable facies, Tertiary *h* sediments can, perhaps, be distinguished from younger rocks by the presence in the latter of *Calcarina spengleri* and *Baculogypsina sphaerulata* (see Todd 1960).

* See Postscript p. 128.

VI. NOTES ON THE MARKER FORAMINIFERA

Genera and species are arranged in alphabetical order throughout this section. The position of each genus and/or species on the range chart is indicated on pp. 129–131.

Actinosiphon punjabensis (Davies). Ta_1. Known from Pakistan, Dhak Pass Beds, Khairabad Limestone, Patala Shales (Davies & Pinfold 1937) and Borneo. The genus is widely distributed, having been described originally from America.

Aktinocyclina. Ta_3–T*b*. Numerous records, but the species are of uncertain stratigraphical value. Possibly only a variant of *Discocyclina*. The genus ranges down into the Lower Eocene of Europe (Banner *et al.* 1967) and may yet prove to have a similar range in S.W. Asia.

Alveolinella. T*f*-Recent. This genus may be represented by one valid species only, *A. quoyi*, which probably evolved from *Flosculinella bontangensis* early in T*f* times.

A. fennemai (Checchia-Rispoli). Lower T*f*. Most of the earliest representatives of *Alveolinella* have either been reported under this name or as *A. borneensis* Tan. However, as neither species has been adequately described or figured it is uncertain how they differ from *A. quoyi*.

A. quoyi d'Orbigny. Upper T*f*-Recent. Confined to the Indo-Pacific region. Probably evolved after the Indian Ocean lost its connection with the Tethys. Recent specimens vary enormously in size and shape.

Archaias. T*d*-Recent. (Range elsewhere : M. Eocene-Recent). A long-ranging and taxonomically difficult genus, the species of which need careful revision on the basis of plentiful matrix-free material. It is doubtful if much reliance can be placed on the ranges normally assigned to the nominal species as they are difficult to tell apart, especially in random sections.

A. operculiniformis Henson. T*d*-Lower T*e*. Only known with certainty from the Lower Asmari Limestone (Eames *et al.* 1962). Its exact range within T*d* is unknown.

A. vandervlerki de Neve. Lower–Upper T*e*. Known from Borneo and Saipan (de Neve 1947 ; Cole 1957), but needs to be redescribed and compared with other species, particularly with *" Taberina " malabarica*. The foraminifera listed by de Neve as occurring with *A. vandervlerki* suggest a very late T*e* or early T*f* age.

Assilina. Ta_1–Ta_3. A widely distributed genus in the Indo-Pacific region. The following species are believed to be short-ranging, at least within the Indian subcontinent.

A. cancellata Nuttall. Ta_3. The largest species so far reported. Believed to be confined to the early Middle Eocene, but as there are few records this species is not shown on Figure 3.

A. dandotica Davies. Ta_1. First described from the Khairabad Limestone and Patala Shales of the Punjab Salt Range (Davies & Pinfold 1937).

A. exponens (Sowerby). Ta_2–Ta_3. Mainly Lower Khirthar but also reported from late Laki beds (upper part of the Ghazij Shales) by Nuttall (1926c : 122).

A. granulosa (d'Archiac) (= *A. leymeriei*). Ta_2. Gill (1953) discussed the stratigraphical distribution of this species, noting that it occurred at all levels in the marine Laki of the Kohat/Potwar Basin. He also demonstrated its relationship to *A. spinosa* Davies which he regarded as a synonym. Nuttall (1926d) suggested

that *A. ranikoti*, *A. granulosa*, *A. exponens* and *A. cancellata* formed an evolutionary lineage in which intermediate forms could be found.

A. spira (de Roissy). Ta_3. Occurs commonly in Pakistan. According to Nuttall (1926d) it is restricted to the upper part of the Middle Khirthar.

Species of *Assilina* are of limited value for dating limestones since oriented sections or matrix-free specimens are usually necessary for the recognition of specific characters.

Asterocyclina. Ta_3–T*b*. Very common in T*b*. Ranges of the species largely unknown except in the Pacific Isles where Cole (1958) has reported several from the lower part of the succession in Eniwetok. At least one species, *A. matanzensis* appears to range throughout T*b*. The earliest known occurrence of *Asterocyclina* in Asia is probably that recorded by Samanta (1965) from the Siju Limestone, Assam, but it occurs throughout the Middle and Lower Eocene of Europe (Neumann 1958) and will doubtless eventually prove to have the same range in the Far East.

Asterorotalia pulchella (d'Orbigny) gr. (= *A. trispinosa* Thalmann). T*g*–Recent. The prominent spines possessed by all the known species of the genus should render it readily recognizable in sections of limestone. Huang (1964) has reported the ancestral forms of *A. pulchella*, (*A. multispinosa* and *A. subtrispinosa*) from the Upper Miocene of Taiwan. It would be difficult, if not impossible, to distinguish between these three species in random sections, so the range of the group is given here.

Austrotrillina ?T*c*, T*d*–Lower T*f*. A small benthic genus readily recognizable in random sections of limestone because of its unusual wall structure. Species recently revised by Adams (1968).

A. asmariensis Adams. ?T*c*, T*d*–Upper T*e*. Best known from the Middle East, but random cuts of limestones from the Indo-Pacific have often yielded specimens indistinguishable from this species. First occurrences are in late Lower or early Middle Oligocene limestones of Iran and Iraq (Adams 1968).

A. howchini (Schlumberger). Late Upper T*e*–Lower T*f*. The most advanced species of the genus. Typically found in Lower T*f* strata over the entire region, and known to have coexisted with *Orbulina universa* through at least the upper part of its range. Transitional forms to *A. striata* occur in the late T*e* limestones of Borneo and Saipan. Last known occurrence is in the Pata Limestone of South Australia.

A. paucialveolata Grimsdale. T*d*. There are few reliable records of this species which was first described from the Shurau Formation, Iraq.

A. striata Todd & Post. T*d*–Upper T*e*. Widespread throughout the Indo-Pacific. Passes into *A. howchini* at high levels in T*e*. First known occurrence is in the late T*d* part of the Melinau Limestone, Sarawak.

Baculogypsina sphaerulata (Parker & Jones). Pleistocene–Recent. A reef dweller (see Cole 1957, Todd 1960, Cole 1963). Indo-Pacific region only.

Biplanispira. T*b*. Common in late T*b* limestones in the Pacific Isles (Cole 1954, 57, 58) ; also found in New Guinea (Crespin 1938), throughout Indonesia and in Burma (Beets 1949). Occurs in the Melinau Limestone, Sarawak (unpublished record). Present evidence suggests that this genus might be absent from early T*b*. It is not known from Pakistan where it was wrongly said to occur by the writer

(1967 ; 200). The ranges of the five nominal species are unknown. This genus is an evolutionary development of *Pellatispira* and may eventually prove to be represented by a single valid species.

Borelis. T*b*–Recent. Common from T*c* times onward in the Indo-Pacific region but apparently no records from Upper T*f*–T*h*. The only authentic T*b* record from the region appears to be that of Cole (1957). Further reports may, however, be expected in the future since it also occurs in the Eocene of the Tethyan region (Schweighauser 1952).

B. melo curdica Reichel. Lower T*f*. Only known from the north-western part of the area (Iraq and Iran. See Thomas 1950 and James & Wynd 1965, Fig. 78, Upper Asmari Limestone and lowest Gach Saran Formation) but very common in the Tethyan region.

*B. melo melo** (Fichtel & Moll). ?U.T*e*–Lower T*f*. Occurs in the Upper Asmari Limestone, Gach Saran Foramations, and basal (Guri Member) of the Mishan Formation according to Eames *et al.* (1962) and James & Wynd (1965). Also known from the Somali Republic (writer's identification), and Kenya (Eames *et al.* 1962, pl. VIIF) where it occurs in association with *Flosculinella bontangensis*. There are no unequivocal records from the East Indies or the Pacific. Cole (1958) found two specimens in Eniwetok drill hole F1 which he assigned to this species, although he admitted (p. 764) that they could not be identified with certainty. They occurred in cored material along with *Miogypsina thecideaeformis*, *Miogypsinoides dehaarti*, *Flosculinella globulosa* and *Gypsina marianensis*, i.e. a typical late Upper T*e* assemblage, and slightly older than the beds in which *B. melo melo* normally occurs in the Mediterranean region.

B. pulchrus (d'Orbigny). Pleistocene to Recent on published evidence, but perhaps ranging down into the Miocene where it may grade into *B. melo*.

*B. pygmaeus** Hanzawa. T*b*–Upper T*e* (most common in T*d* and Lower T*e*). Cole (1957) figured a specimen from the Upper Eocene of Saipan. This record is almost unique, the only other from T*b* strata in the Indo-Pacific being that of Caudri (1934) who reported *N.* cf. *pygmaea* from probable T*b* rocks of West Soemba. Henrici's (1934) records from the Lower Eocene of Timor are probably all incorrect since his illustration (pl. 3, fig. 1) is clearly of *Fasciolites* s.s. and not of *Borelis*. Adams (1965) illustrated this species from the T*c* part of the Melinau Limestone, Sarawak. There are many Lower–Upper T*e* records (e.g. Cole 1957).

*B. schlumbergeri** (Reichel). T*g*–Recent. There are two doubtful records from Bikini drill hole 2A (Cole 1954 and Todd & Post 1954). It has been reported from the T*g* part of cores from Eniwetok Atoll (Cole 1958). This species may be gradational to *B. pulchra* as believed by Hofker (1952) but the evidence for this is as yet inadequate. All the other described post-Eocene species (e.g. *B. parvulus*, *B. primitivus*, *B. philippinensis*) except *B. inflata* (Adams), which is known only from T*c*, occur within T*e*—probably all within Lower T*e*—but their relative positions and ranges are unknown.

Boreloides eniwetokensis Cole, T*b*. A rather striking species, so far known only from Eniwetok Atoll but almost certain to be found elsewhere in the future. Other

* See Postscript p. 128.

records of the genus are all from the Americas, as indicated by Hanzawa (1962).

Bullalveolina bulloides (d'Orbigny) emend. Reichel. T*d*. Only reported from the Asmari Limestone (James & Wynd 1965) and never figured or described.

Calcarina spengleri (Linné). Pleistocene–Recent. A reef dweller restricted to the Indo-Pacific region. (See Cole 1957, 1963, and Todd 1960.)

Chapmanina. T*b*. Known from East Africa and Iran (e.g. Eames *et al.* 1962, James & Wynd 1965) and several times reported from Indonesia but never figured or described. Records of species from Borneo checked by the writer have proved to be erroneous. It is possible that this essentially Tethyan genus, the earliest record of which is from the Middle Eocene (= Ta_3), did not reach the Far East. Schweighauser (1953) reported it from the Lower Eocene of Italy.

Coskinolina. Lower Cretaceous–T*b*. Most species difficult to recognize in random sections. A few Tertiary forms may be potentially valuable as stratigraphical markers.

C. rotaliformis Cole. T*b*. Described (1958) from late T*b* beds, Eniwetok Atoll.

Cycloclypeus. T*c*–Recent. One of the most studied of all the larger foraminifera but still inadequately known from good stratigraphic sections. The embryonic apparatus shows marked evolutionary changes with time (Tan 1932; Drooger 1955 ; MacGillavry 1962). Specific differences are very arbitrary and often difficult to maintain. Commonly occurring species are :

C. carpenteri Brady (including *C. guembelianus* Brady). Upper T*f*–Recent. Reliable T*f* records are few, but van der Vlerk (1961) reported it from late T*f* beds in Java together with the holotype of *Lepidocyclina radiata*, and Cole (1963) reported it from the upper part of the Alifan Limestone of Guam.

C. eidae Tan. Lower T*e*–T*f*. Evolved from the T*c*/*d* *C. koolhoveni*/*oppenoorthi* group. Although there are numerous records from the area, the exact level of the first appearance is unknown. It has not been found in the lowest T*e* beds of the Melinau Limestone. Tan (1932) and Drooger (1955 : 416) have reported it from Lowest T*f*.

C. indopacificus Tan. ?Upper T*e*, Lower-Upper T*f*, ?T*g*. A species frequently reported from Lower T*f* (e.g. Caudri 1932 : 173). Exact range uncertain. Cole (1957) tentatively assigned a specimen from the Tagpochau Limestone of Saipan to this species. At the upper end of its range it grades into *C. postindopacificus* and *C. carpenteri*. Caudri (1932 : 176) reported it from beds said to be younger than Tertiary *f*.

C. koolhoveni Tan. T*c*. Originally described (1932) from the Lower Oligocene of Java and not subsequently reported elsewhere in the Far East. It is the most primitive cycloclypeid and quite easily recognizable. Its exact range is unknown but it must grade into *C. oppenoorthi* at or about the T*c*/*d* boundary.

C. oppenoorthi Tan. T*d*–?basal Lower T*e*. Believed to be a marker for T*d* but must grade downwards into *C. koolhoveni* and upwards into *C. eidae*. The only verifiable records appear to be those of Tan (1932). The ?T*e* record is from Tjiapoes, Bantam, Java (see Tan, table V).

C. posteidae Tan. Upper T*e*–Lower T*f*. Common in Lower T*f*. Level of first

appearance unknown, but Cole (1957) figured a good specimen from an unknown horizon in the Upper T*e* limestones of Saipan.

C. postindopacificus Tan. Not distinguished here from *C. carpenteri* and not, therefore, on the chart.

C. (*Katacycloclypeus*). ?Te_5–Lower T*f*. This subgenus contains several nominal species which, with the possible exception of *C.* (*K*) *annulatus*, are believed to be restricted to Lower T*f*.

C. (*K.*) *annulatus* Martin. ?Upper T*e*–Lower T*f*. Mainly Lower T*f*, but also reported (not figured) from the Djonggrangan beds of probable Upper T*e* age in central Java (van Bemmelen 1949). At the upper end of its range it has sometimes been recorded (e.g., Cole 1945) in association with *Lepidocyclina rutteni*.

C. (*Radiocycloclypeus*) *radiatus* Tan (= *C. stellatus* Tan). Lower–Upper T*f*.

C. radiatus is the pillared form of *C. stellatus*. Tan gave the range of *R. stellatus* as Burdigalian–Vindobonian. The difference between *C. radiatus*/*stellatus* and *C. carpenteri*/*guembelianus* is merely one of shape (Tan 1932 : 92) and is of no known biological significance.

Dictyoconoides. Ta_1–Ta_3. A rather striking genus so far known only from the western part of the region (Africa and Pakistan). This apparent geographical restriction may, however, be due to the paucity of information on Lower and Middle Eocene carbonate sediments in south-east Asia.

D. flemingi Davies. Ta_1. Range based on information given by Davies & Pinfold (1937) ; known from the Punjab Salt Range and Tibet.

D. cooki (Carter). Ta_{2-3}. Numerous records from the Middle Eocene. Gill (1949) showed *D. cooki* to be a senior synonym of *D. kohaticus* Davies and gave its range as Upper Laki (Ta_2) through the Middle Khirthar. Samanta (1965) reported it from the lower part of the Siju Limestone.

Dictyoconus. Lower Cretaceous–T*c*. Species difficult to separate in random sections of limestones. Most Palaeogene forms occur in the Lower and Middle Eocene.

D. melinauensis Adams. T*c*. A structurally simple form known only from the Melinau and Bukit Sarang limestones in Sarawak.

Discocyclina. Ta_1–T*b*. A widespread genus represented by numerous nominal species, the final extinction of which is usually taken to mark the end of the Eocene in the Indo-Pacific region. The earliest representatives are apparently all rather small, the largest species occurring in the Middle Eocene and early Upper Eocene. Samanta (1969) has reviewed the Indian species, and these are now much better known than those from the East Indies. A few of the more important forms are mentioned below.

D. archiaci (Schlumberger). T*b*. Published records suggest that this is a very long-ranging species but the Palaeocene to early Eocene reports from the Indian area are now thought to be incorrect (Samanta 1965, 1969).

D. dispansa (Sowerby). Ta_3–T*b*. Believed to be restricted to the Middle and Upper Eocene (Sen Gupta 1963 and Samanta 1965). One of the earliest records is certainly that of Nuttall (1926c).

D. javana (Verbeek). Ta_3–early T*b*. Middle to Upper Eocene in the Indian region (Samanta 1965) ; also occurring in T*b* (base of the Bukit Besungai limestone)

Sarawak (Adams 1960: specimens deposited in the B.M. (N.H.), register number P 45151).

D. omphalus (Fritsch). Ta_3–T*b*. Very widespread. Mainly T*b* but also occurring in the late Middle Eocene (Ta_3) of India according to Samanta (1969).

D. ranikotensis Davies. Ta_{1-2}. One of the earliest species, and not so far known outside West Pakistan where it occurs in the highest Ranikot and lowest Laki beds of the Salt Range.

D. sella (d'Archiac). ?Ta_3–T*b*. Upper Eocene only in the Indian region according to Samanta (1969), but also frequently reported from the Middle Eocene of the Tethyan region.

D. sowerbyi Nuttall. Ta_3–T*b*. Middle to Upper Eocene in the Indian region (Samanta 1965, 1969), and reported from Ta_3 beds in Java (van Bemmelen 1949 : 105).

D. undulata Nuttall. Ta_3. Apparently restricted to the Middle Eocene in the Indian region (Samanta 1969). Nuttall (1926c) reported it from the lower part of the Middle Khirthar, and this record has been accepted by later authors.

Fabiania. Ta_3–T*b*. The first known appearance in the region is in the Prang Stage sediments of Assam, Wilson & Metre (1953). Its last known occurrence is at the top of the T*b* part of Melinau limestone, Sarawak. *F. saipanensis* Cole is the commonly reported T*b* species in the Indo-Pacific.

Fasciolites. (= *Alveolina*). Ta_1–Ta_3. A distinctive genus containing many nominal Indo-Pacific species all of which are in need of revision. *F. vredenburgi* Davies seems to be the first species known from the region. It occurs in the Khairabad Limestones and Patala Shales of the Salt Range. Hottinger (in press) has recognized *F. cucumiformis* in beds of Upper Ranikot age in Sind. The last species to become extinct was probably *F. elliptica* var. *nuttalli* Davies (Kohat Shales and other Middle Eocene horizons, e.g. the lower part of the Siju Limestone, Assam). Commonly reported species are: *F. elliptica* Sowerby—possibly restricted to the Middle Eocene and considered by Eames (1952) to be a synonym of *F. ovoidea—F. globosa* (Leymerie), *F.* (*Glomalveolina*) *lepidula* (Schwager), *F. oblonga* (d'Orbigny), *F. ovoidea* (d'Orbigny), *F. subpyrenaica* (Leymerie), *F. timorensis* (Verbeek) and *F. wichmanni* Rutten. *F. wichmanni* commonly occurs with *Lacazinella, Assilina* and/or *Nummulites javanus*, an association which strongly suggests a late Ta_3 age.

Bakx (1932) discussed the ranges of the various species of *Fasciolites* and *Neoalveolina* in the Indo-Pacific region, and so far as the former is concerned there is little that can be added today. However, the ranges he quoted for *F. javanus* and *F. wichmanni* were certainly incorrect. Neither species is known from T*b* or T*c*.

Flosculinella. Upper T*e*–Lower T*f*. A widespread and short-ranged genus of great stratigraphical value.

F. bontangensis (Rutten). ?Upper T*e*–Lower T*f*. Believed to be restricted to Lower T*f* and to have evolved from *F. globulosa*. One of the earliest appearances of the species is in the orbitoidal limestones of Christmas Island (Ludbrook 1965) where

it occurs immediately above beds with an Upper T*e* fauna (Adams & Belford: paper in preparation). Mohler (1947) reported *F. bontangensis-globulosa* in association with *Miogypsinoides dehaarti* and an assemblage of lepidocyclines dated as Tf_1. This material must certainly have come from very close to the T*e*/T*f* boundary. *F. bontangensis* may have been extinct before the end of Lower T*f*. It is known from East Africa (Eames *et al.* 1962) to the Pacific Islands. *Alveolina cucumoides* Chapman is a junior synonym.

F. globulosa (Rutten). Upper T*e* — ?Lower T*f*. Grades into *F. reicheli* at the lower end of its range as shown by Mohler (1949) and into *F. bontangensis* at the upper end. It is not certain whether the transition to *F. bontangensis* occurs immediately below or just above the T*e*/T*f* boundary.

F. reicheli Mohler. Upper T*e*. The first appearance of this species marks the base of Upper T*e* in some successions, e.g. the Melinau Limestone (Adams 1965). It grades upwards into *F. globulosa* according to Mohler (1950).

Gypsina. Eocene—Recent. A long-ranging genus with only one species of sufficient interest to merit inclusion here.

G. marianensis Hanzawa. Upper T*e*. First described from Saipan but subsequently found in beds of the same age in Eniwetok, Guam and Christmas Island.

Halkyardia. Ta_3–Lower T*e*. Numerous records from the whole area. The earliest verifiable occurrence seems to be *H. minima* var. *indica* from the Lutetian (Ta_3) of Cutch (Tewari 1956). The writer (1967) noted that the genus is known from several Lower T*e* limestones in Borneo.

Heterostegina. Ta_1–Recent. A very long-ranging genus. It is doubtful if any of the Indo-Pacific Eocene and early Oligocene species are sufficiently well known or diagnostic to be of stratigraphical value, although names such as *H. ruida, H. reticulata* appear constantly in the literature. The following are of proven stratigraphical value:

H. bantamensis Tan. T*c*. This species differs from *H. praecursor* Tan in the presence of an umbonal pillar (Tan 1932). Both were originally described from the Lower Oligocene of Java and are believed to be ancestral to *Cycloclypeus*.

H. borneensis van der Vlerk. ?T*d*–Lower T*e*. ?Upper T*e*. Very widespread in Lower T*e*. Although Rickwood (1955) and Visser & Hermes (1962) have reported this species from T*c*/*d* and T*d* beds respectively in New Guinea (no figures or descriptions given), evidence from the Melinau limestone, Sarawak, suggests that it does not extend down to the base of T*e*. It does, however, appear before *Spiroclypeus* in this particular sequence. Leupold and van der Vlerk (1931) recognized that *H. borneensis* appeared before *Spiroclypeus* in T*e*, when they stated (p. 626) that within the Tidoengsche Landen of eastern Borneo " in the deepest horizons of stage *e* ", they were referring to the Mesaloi marls (about 1,000 metres thick), " no real *Spiroclypeus* is found, although strongly evoluted heterosteginae (*Heterostegina borneensis*) do occur ". They regarded *H. borneensis* as a marker for Te_1 although they had not at that time examined faunas from a continuous T*d*–T*e* succession. Van der Vlerk's record (1966) of *H. borneensis* in association with *L.* (*N.*) *isolepidinoides* from an isolated sample from East Borneo is very interesting since it apparently proves that the ranges of these two species overlap. There are

reports of this species from Upper T*e* strata (e.g., Rickwood 1955) but they have never been confirmed by figures or descriptions.

H. saipanensis Cole. T*b*. First described (1953: see Cole & Bridges) from Saipan and subsequently reported from Christmas Island (Ludbrook 1965).

Future work may show that other species of *Heterostegina* have restricted ranges.

Lacazinella. Ta_3–T*c*.

Lacazinella reicheli Bursch. T*b*–T*c*. So far known only from the Moluccas. Some authors have questioned the reliability of Bursch's Tertiary *c* determination, but examination of his material in Basle University has confirmed that this species occurs in abundance with well preserved *Nummulites fichteli* in some samples.

L. wichmanni (Schlumberger). Ta_3–T*b*. ?T*c*. Known only from the New Guinea area (Rutten 1914, 1936, Bursch 1947, Rickwood 1955, Crespin 1962). Exact range within T*b* uncertain, but certainly occurring in the lower part since it has been found in Ta_3 beds with *Fasciolites* and *Nummulites javanus* (Rutten 1936, Crespin 1962). The T*c* record (Bursch 1947, Table 1) is doubtful.

Lepidocyclina. T*d*–Upper T*f*. This genus contains a larger number of nominal species amongst which are many synonyms. There is little reliable information about the morphological variation or ranges of most of the species. *Lepidocyclina* appeared suddenly in the Far East having migrated there from the Americas, probably by way of the Tethys (Adams 1967); the genus finally became extinct in the late Miocene.

Cole (1962) commented that the subgeneric divisions of *Lepidocyclina* cannot properly be maintained. He was almost certainly right in thinking that they have no biological significance. On the other hand, they still have a certain practical value in stratigraphy and may be retained until the age-diagnostic species have been more carefully described and have had their ranges verified.

Lepidocyclina (*Eulepidina*). T*d*–Upper T*e*. The occurrence of this subgenus in association with *Nummulites* defines T*d*. It was very abundant throughout Lower T*e* and became extinct at, or just prior to, the end of Upper T*e*. A few of the best-known species are listed below, but are not included on the range charts for the reason given above.

L. (*Eulepidina*) *dilatata* (Michelotti). This species was originally described from the Lower Miocene of Italy, but the name has often been applied uncritically to Oligocene forms in the Far East.

L. (*Eulepidina*) *ephippioides* Jones & Chapman. First described from the "Miocene" orbitoidal limestones of Christmas Island, and subsequently used as a "sack name" for almost any *Eulepidina*. The types are now known to have come from late Lower T*e* strata (Adams & Belford: paper in preparation).

L. (*Eulepidina*) *formosa* Schlumberger. First described from an unknown level in T*e* strata of Borneo. This species, although well described and illustrated, is unfortunately predated by the rather poorly described *Lepidocyclina* (*E.*) *ephippioides*.

L. (*Eulepidina*) *papuaensis* Chapman. Originally described from beds of Lower T*e* age in New Guinea. This name, like *E. dilatata*, has since been applied indiscriminately to T*d* species.

The subgenus *Eulepidina* is in great need of revision and, in the writer's opinion,

it is not at present possible to distinguish satisfactorily between one nominal species and another.

Lepidocyclina (*Nephrolepidina*). T*d*–Upper T*f*. It is not known whether or not this subgenus ranges right down to the base of T*d*, but it is almost certain that it does not extend to the top of T*f*. However, since T*g* is normally defined by the absence of *Nephrolepidina*, its occurrence high in T*f* has at present to be assumed.

L. (*N.*) *ferreroi* Provale. ?Late Upper T*e*–Lower T*f*. A readily determinable species largely restricted to Lower T*f*. Although there are numerous records (e.g., Caudri 1932, 34, 39) from strata of this age, there is no way of determining which are the oldest and youngest. Tan (1932) listed *N. ferreroi* together with *Eulepidina* and *Cycloclypeus eidae* from Paloe Soreng, Borneo, but this determination cannot be verified as there is no figure or description. Hanzawa (1957, Table 2) reported it from the Tagpochau Limestone, Saipan, in association with *Eulepidina formosa*.

L. (*N.*) *inflata* Provale (B form is *L. acuta*). Upper T*e*–Lower T*f*. Numerous records. Particularly common in the Upper T*e* limestones of the Kinabatangan River, Sabah (personal observation).

L. (*N.*) *isolepidinoides* van der Vlerk. T*d*–early Lower T*e*. The most primitive species known from the East Indies, and originally described from beds of Lower T*e* age. It occurs commonly in T*d* and early T*e* strata, and in the latter grades into *N. parva*. Van der Vlerk (1966) reported *N. isolepidinoides* in association with *Heterostegina borneensis* and *Eulepidina*, an assemblage believed by the writer to be indicative of early Lower T*e*.

L. (*N.*) *japonica* (Yabe). Upper T*e*–Lower T*f*. Reported from unknown levels in Upper T*e* by van der Vlerk (1929) and Krijnen (1931), and by numerous authors from Lower T*f* beds in the region.

L. (*N.*) *martini* (Schlumberger). ?Upper T*e*–Lower T*f*, ?Upper T*f*. Very common in Lower T*f*. Caudri (1939 : 139) has reported, but not figured, this species from an assemblage that can be dated as Upper T*e* on the presence of *Spiroclypeus* and *Eulepidina*. There are also other records from beds of Upper T*e* age but the writer has been unable to verify them. The morphological limits of *N. martini* appear to be as uncertain as its stratigraphical range. It may range up into beds of late T*f* age.

L. (*N.*) *parva* Oppenoorth. T*d*–Lower T*e*. Upper T*e*–?Lower T*f*. A descendant of *N. isolepidinoides*, common in late T*d* and Lower T*e* beds. The upper limit of this species is uncertain as it has been reported from Upper T*e* strata on Saipan and in cored material of supposed T*f* age (see p. 97) from the Bikini drill holes (Cole 1957 & 1954).

L. (*N.*) *sumatrensis* (Brady) & vars. Lower T*e*–Lower T*f*. This species is most common in Upper T*e* and Lower T*f* sediments. It probably evolved from *N. parva* in late T*e* times. Caudri (1939) and Cole (1958) have suggested that *N. parva* is a junior synonym of *N. sumatrensis*. However, combining the two species merely obscures the stratigraphical value of the first and last members of the series without providing any compensatory benefits.

L. (*N.*) *verbeeki* Newton & Holland. Upper T*e*–?Lower T*f*. Commonly encountered in strata of late Upper T*e* age (e.g., l'Isle de Nias, Douvillé 1912; Saipan, Cole 1957).

Also widely reported from Lower T*f* (e.g., Leupold & van der Vlerk 1931 : 632), but these age determinations are difficult to verify. There appears to be no proof that this species ranges up into Lower T*f* although it may well do so.

Many other species of *Nephrolepidina* are of potential stratigraphical value, but their ranges cannot at present be determined with sufficient accuracy for them to be worth recording here. *N. angulosa* (Provale), *N. brouweri* Rutten, *N. borneensis* Provale and *N. verrucosa* Scheffen have all been reported from Upper T*e* and Lower T*f* sediments.

In a series of papers extending over the last decade, van der Vlerk (1959–68) has shown that in *Nephrolepidina* the proloculus becomes progressively more highly embraced by the deuteroconch with time. He has expressed this numerically and used it for dating samples containing sufficient specimens for the results to be statistically reliable. The writer recently tested this method on topotype specimens of *N. verbeeki* from Sumatra, on Lower and Upper T*e* assemblages of *N.* cf. *parva* from the Kinabatangan River, Borneo, and on a population of *N. howchini* Crespin from the Batesford Limestone, Victoria, Australia. Good results were obtained from the Sumatran and Australian samples, each of which contained only one species, but the results from the Bornean samples, which contained more than one species, were contradictory and meaningless. It seems that the method requires further refinement before it can be applied generally.

Lepidocyclina (*Tribliolepidina*). T*f*. This subgenus comprises only a few species, the most important of which are:

L. (*T.*) *orientalis* van der Vlerk. Lower T*f*–Upper T*f*. First described from the Njalindung beds of Java (late Lower T*f* or early Upper T*f*) and subsequently reported from Upper T*f* beds elsewhere. Certain age determinations based solely on the occurrence of this species may be incorrect, e.g., Cole (1954 & 58) since, as stated earlier, it is likely that Upper T*f* is not represented in the Bikini and Eniwetok drill holes. Cole (1954) believes *L. talahabensis* van der Vlerk to be a junior synonym. The types of both species come from the same locality.

L. (*T.*) *radiata* Martin. Lower T*f*–Upper T*f*. According to van der Vlerk (1961) the types come from the late T*f* of Java. This age determination was, however, based partly on the evolutionary stage reached by the embryonic apparatus and cannot, therefore, be accepted without reservation. There is as yet no objective stratigraphical or palaeontological evidence to prove a late T*f* (Tf_3) age for the types. Cole (1960) placed eight species in synonymy with *L. radiata* and even if only three of these (*L. suvaensis*, *L. fijiensis* & *L. oneatensis*) are accepted as synonyms, the effect is to increase the range of *L. radiata* to the whole of T*f*.

L. (*T.*) *rutteni* van der Vlerk. Lower–Upper T*f*. First reported from the Tji Lanang beds, uppermost T*f*, of Java. Also found occasionally in Lower T*f* assemblages as indicated by Caudri (1932). Level of extinction unknown.

L. (*T.*) *talahabensis* van der Vlerk. Late Lower–Upper T*f*. Originally reported from Java, and subsequently from the Barito Basin, Borneo, in beds said to be Tf_{2-3} in age (van der Vlerk 1966). However, since the dating of these beds depends on the presence of this species, their age cannot be verified. (See *L.* (*T.*) *orientalis*.)

Lepidocyclina. T*d*–T*f*. The microspheric forms of most species are commonly referred to simply as *Lepidocyclina*, since it is difficult to know which subgenus and species each represents.

L. acuta (Rutten) Upper T*e*–Lower T*f*. Probably the megalospheric form of *N. inflata* Provale, although the two are not always found together.

L. flexuosa Rutten. Upper T*e*–Lower T*f*. Exact levels of first and last occurrences unknown, but very common in both stages.

Linderina. Ta_2–T*b*. Widespread and common. Silvestri (1942) reported it from the Lower Eocene of Somaliland. Elsewhere in the region, the first known appearances are in the Prang Stage sediments of Assam (Wilson & Metre 1953), in limestones from Rajasthan, India (Singh 1953) and in the Kohat Shales, Pakistan (Eames 1952). This genus also occurs in association with *Pellatispira* in the Upper Chocolate Clays of the Sulaiman Range, Pakistan. These specimens have never been described, but are deposited in the British Museum (Natural History), register numbers P 48503–7 (Siddiqui collection). Records of *Linderina* from Lower T*e* limestones of Borneo are either due to errors in determination of *Miogypsinoides* and/or *Planorbulinella* (e.g., Newton & Holland 1899), or else represent reworked Eocene specimens as at Keramit (Adams & Wilford : in press).

Lockhartia. Ta_1–Ta_3. So far only described from the western part of the region. First occurrence appears to be in the Dhak Pass Beds, Pakistan (Davies & Pinfold 1937). Nagappa's record (1959, Table 6 & Chart 1) from the Upper Eocene of Pakistan is believed to be incorrect since he quotes as his authority Eames (1952) who makes no mention of this genus from the Upper Chharat beds of Kohat. These beds are, in any case, regarded as Middle Eocene by most authors. Silvestri (1942) described *L. alveolata* from the Middle Eocene of Somaliland.

Marginopora vertebralis Blainville. Upper T*e*–Recent. Very common during and after Upper T*f* times. Level of the first appearance difficult to ascertain as the genus can be confused with *Sorites* in random sections of limestone. Cole (1957, pl. 103) figured two specimens from the Tagpochau Limestone (T*e*) of Saipan, but in the writer's opinion they could have been assigned to *Sorites*. On the other hand, Hanzawa (1957, pl. 6, fig. 7) figured a good vertical section from the Upper T*e* part of the Tagpochau Limestone on Tinian Island which is also part of the Mariana group. This specimen occurred in association with *Miogypsina* spp. and *Gypsina marianensis*. *M. vertebralis* has often been reported from Lower T*f* limestones, e.g., the Tulki and Trealla limestones of Australia (Crespin 1955).

Meandropsina anahensis Henson. Upper T*e*–mid.Lower T*f*. Known from the Middle and Upper Asmari Limestone and from the lower part of the Gach Saran Formation.

Miogypsina. Upper T*e*–Lower T*f*. ?Upper T*f*. This genus includes a considerable number of nominal species, the ranges of which are uncertain. It appeared in the Indo-Pacific region at the beginning of Upper T*e* times and was probably extinct by Upper T*f*. Unfortunately, it is not possible even to determine the youngest record with any degree of confidence. Drooger (1963) indicated that it is *M. antillea* (= *M. tuberosa* in the East Indies), but the evidence for the age of the type specimens is very poor. Caudri (1932) reported "*tuberosa*" from Javanese

assemblages including *Lepidocyclina rutteni*, *Cycloclypeus annulatus*, *C. neglectus* var. *indopacifica* and other miogypsinids, an association suggesting that the beds were not younger than Lower T*f*. On the other hand, Banner *et al.* (1967) gave the last record as *M. subtilis* (= *M. cushmani* var. *subtilis*) from the Bentang Series of Java, which they claim is Middle Miocene in age. Van Bemmelen (1949) said that this Series was " Young Miocene " in age. Unfortunately, there is no way of checking this determination. Clarke & Blow (1969 : 88, 89) quoted *M. indonesiensis* Tan as the last known representative of the genus in the Far East. They claim that it occurs in Tf_3, but the weight of stratigraphical evidence strongly suggests a Tf_{1-2} age. The youngest record which the present writer regards as acceptable is of specimens from the Njalindung beds of Java (late Lower or early Upper T*f*).

There appears to be no reliable evidence to support the belief that *Miogypsina* occurs in Upper T*f*, although there are records in the older literature (e.g., *M. epigona* Schubert from the Bismark Archipelago: Schubert 1910 & 1911) of *Miogypsina* occurring in association with *Orbulina* and *Globorotalia menardii*.

M. thecideaeformis (Rutten). Upper T*e*–Lower T*f*. This is one of the most commonly reported Upper T*e* species, along with *M. kotoi* Hanzawa, *M. neodispansa* (Jones & Chapman) and *M. irregularis* (Michelotti). *M. excentrica* Tan and *M. polymorpha* (Rutten) certainly occur in Lower T*f* as do others that continue up from T*e*.

Miogypsinoides (including *Miogypsinella*). ?T*d*, Lower T*e*–Lower T*f*. The earliest occurrence is that reported by Tan (1932, no figure or description given) from Java. There are no other T*d* records. However, since the genus occurs in the Middle Oligocene of the Tethyan region (Drooger 1963) it might well be expected in beds of the same age in the Far East.

M. bantamensis Tan*. Late Lower T*e*. This species occurs in beds a little older than those with *M. dehaarti* on Christmas Island (Adams & Belford : paper in preparation) and in a deep well on Kita-Daitô-Zima (Hanzawa, 1940).

It appears that *M. bantamensis*, *M. lateralis* Hanzawa and *M. borodinensis* (Hanzawa) all occur at high levels in the Lower T*e* limestones of Saipan (Hanzawa 1957 & Cole 1957), but the ranges of the individual species are unknown.

M. complanatus (Schlumberger) (including *M. ubaghsi* Tan). ?T*d*, Lower T*e*. Although the published records are unreliable this is nevertheless the probable range of the species since it agrees well with the range in Europe. The writer has seen this species in late Lower T*e* beds of Christmas Island and in various Lower T*e* limestones (e.g., Keramit, exact horizon unknown) in Borneo. Adams (1965) reported it from the Lower T*e* part of the Melinau limestone, but the older records on which this occurrence was based have since been checked and found to be erroneous.

M. cupulaeformis (Zuffardi-Comerci). Upper T*e*–Lower T*f*. Originally described (1929) from beds which can be dated as Upper T*e* from the associated faunas (*Spiroclypeus*, *Miogypsina*, *Eulepidina* etc.). Although Cole (1954 & 1958) reported this species from the youngest " T*f* " limestones of Bikini and Eniwetok, there seems to be no real evidence that these beds are younger than early T*f* in age.

* See Postscript p. 128.

Diagnostic T*f* species such as *Alveolinella quoyi, Flosculinella bontangensis,* true *Austrotrillina howchini* and *Lepidocyclina rutteni* are all absent. *M. cupulaeformis* was, however, found with diagnostic Lower T*f* species in the Bonya Limestone, Guam (Cole 1963). Drooger (1953) and van der Vlerk (1966a) were almost certainly correct in regarding the type specimens of this species as synonymous with *M. dehaarti,* in which case Cole's T*f* specimens may require a new name.

*M. dehaarti** van der Vlerk. Upper T*e*. (Also early Lower T*f* according to some authorities, e.g. Mohler 1947; Eames *et al.* 1962, but never figured from beds of this age.) The *Lepidocyclina* species associated with Mohler's specimen certainly suggest an early T*f* age. Widespread over the region and normally a good marker for Upper T*e*. See also *M. cupulaeformis.*

The types of *M. dehaarti* came from the island of Larat, Moluccas, and were associated with numerous planktonic foraminifera including *Globigerina binaiensis, Globigerinoides quadrilobatus primordius, Globoquadrina altispira* and *Globorotalia kugleri* (van der Vlerk 1966a, 1968b), an assemblage clearly indicative of Blow's Zone N4. In the writer's opinion, Zone N4 must straddle the Lower/Upper T*e* boundary since the *Globigerinoides quadrilobatus* group of planktonic foraminifera had certainly made its appearance in the Far East before *M. dehaarti* evolved.

Miscellanea. Ta_1.

M. miscella (d'Archiac & Haime). Ta_1. Reported by Davies & Pinfold (1937) from the base of the Dhak Pass beds to the top of the Patala Shales, Punjab Salt Range, Pakistan. This species has been reported, but never figured or described, from Palaeocene beds of Indonesia. However, the identification of specimens from the Engkilili Formation, Lupar Valley, Sarawak (see Liechti *et al.* 1960 : 55) has been confirmed by the writer. Bursch's record of *M. miscella* from T*b*, T*c* and Lower T*e* beds on Gross Kei can be discounted since his figured specimens could equally well be of *Elphidium* or some closely related genus.

Neoalveolina. (See *Borelis.*)

Nummulites s.s. Ta_1–T*d* (T*a*–Recent *sensu* Treatise on Invertebrate Paleontology). This genus includes a large number of nominal species, many of which are of doubtful validity and uncertain stratigraphical value. It is at present impossible to determine the ranges of most Indo-Pacific species accurately and only a few of the most valuable are listed here. Striate species range from Ta_1–T*d* and are commonest in Ta_2–T*b*. Reticulate forms are unknown from the region before T*b* and are commonest in T*c* and T*d*. Species such as *N. lahiri,* so far known only from Pakistan, are not included on this chart, nor are such long-ranging species as *N. semiglobulus* and *N. mamilla.*

N. atacicus Leymerie. Ta_{2-3}. Numerous records from Laki and Lower to Middle Khirthar rocks. The paucity of carbonate sediments of the right age probably accounts for the non-discovery of this species in the East Indies.

N. carteri d'Archiac & Haime. Ta_3. Believed to be restricted to the upper part of the Middle Khirthar. Few records (e.g., Nuttall 1926c).

N. chavannesi de la Harpe. T*b*. Reported from the western part of the region, e.g. Somaliland (Silvestri 1938) and by Samanta (1968b) from the Kopili Formation,

* See Postscript p. 128.

Garo Hills, Assam. There is also an unpublished record by Bayliss from West Pakistan (see Samanta *op. cit.*).

N. fabianii (Prever). T*b*. There are as yet very few records of this important marker from the central and eastern parts of the region. However, it is known from the Upper Eocene of East Africa (Azzaroli 1952; Eames *et al.*, 1962) and from Assam (Samanta 1968b). It is known to overlap with *Orbitolites complanatus* in Africa (Azzaroli 1952).

N. fichteli Michelotti. T*c*–T*d*. Very widespread and almost certainly derived from the Upper Eocene *N. fabianii*, from which species it can be difficult to distinguish at very low levels in the Oligocene (Adams 1965).

N. gizehensis (Forskål). Ta_3. This well-known species is usually regarded as diagnostic of the Middle Eocene. Samanta (1965) reported it from the upper part of the Siju Limestone, Assam, which he dated as early Upper Eocene (basal T*b*), but later (1968a) regarded as transitional from Middle to Upper Eocene.

N. javanus Verbeek. Ta_3–?basal T*b*. The commonest large species of *Nummulites* in Indonesia, and believed by some to be synonymous with *N. perforatus*. The megalospheric form has often been recorded as *N. bagelensis* Verbeek. The ?T*b* occurrences are at the base of the Bukit Besungai Limestone (Adams & Haak 1962) and the base of the Melinau Limestone, Sarawak (Adams 1965).

N. millecaput Boubée. Ta_3. So far known only from the western end of the region. Davies (1940b) said that this species occurs in the uppermost Lutetian of the Indian region, but Nagappa (1959, Chart 3) extended its range into the Upper Eocene. However, reference to Eames (1952) shows that there is no evidence to support the Upper Eocene part of the range.

N. nuttalli Davies (= *Ranikothalia nuttalli*). Ta_1. Well known from Pakistan. The only verifiable record from Indonesia, that of Van der Vlerk (1929) was disputed by Caudri (1934) who renamed the Bornean species *N. borneensis*. The writer, having sectioned one of Davies' paratypes (P 39407 B.M.N.H.), agrees with Caudri that van der Vlerk's specimens are not the same as those from Pakistan.

N. pengaronensis Verbeek. Late Ta_3–T*c*, ?T*d*. Numerous T*b* records. Samanta (1968b) noted that it occurs in the lower part of the Siju Limestone, i.e., Ta_3 in Assam. Van der Vlerk (1929) reported and figured this species from beds of T*c* age in Borneo. The T*d* report is that of Eames *et al.* (1962), whose record was based on a single specimen from a muddy sandstone. The possibility of reworking cannot be discounted in this instance.

N. thalicus Davies. Ta_1. Best known from Pakistan. Unlike Caudri (*op. cit.*), the writer accepts van der Vlerk's identification of this species from Borneo.

N. vascus Joly & Leymerie. T*c*–T*d*. This is a commonly reported species from the Middle East where it occurs in strata of Lower and Middle Oligocene age. It is also known from Tanganyika (Eames *et al.* 1962 : 67). There are records of this species in beds of Upper Eocene age in the Mediterranean region, but to the best of the writer's knowledge it has not been found in strata of this age in Indonesia.

Operculina (including *Operculinella* & *Operculinoides*). Ta_1–Recent. The species of this long-ranging genus are, on the whole, difficult to recognize with certainty, particularly in random sections of limestone. However, it is possible that species

such as *O. rectilata* (Cole), Tg of Guam and post-Miocene of Bikini, *O. lucidisutura* Cole and *O. amplicuneata* (Cole) may eventually prove to be of some value.

O. canalifera d'Archiac. Ta_1. According to Davies & Pinfold (1937) this species ranges from the base of the Dhak Pass beds to the top of the Patala Shales in the Punjab Salt Range. Specimens very like it occur in the Bukit Asi Limestone, Baram River, Sarawak.

O. salsa Davies (B form is *O. subsalsa* Davies) Ta_1. Occurs throughout the Ranikot beds of the Punjab Salt Range according to Davies & Pinfold (1937).

O. sindensis Davies. (= *Sindulites* Eames 1968) Ta_1. First reported from the highest Ranikot beds at Thal and subsequently from beds of the same age elsewhere.

Opertorbitolites. Ta_{1-2}. The common species *O. douvillei* is fairly widespread in beds of Laki age. Gill (1953) reported *Opertorbitolites* sp. (not. *O. douvillei*) from the Lower Eocene of the Punjab Salt Range. The writer has seen it in the Ranikot beds of Dunghan Hill, Pakistan, and in Ta_1 limestones in Sarawak.*

Orbitolites complanatus Lamarck. Ta_2–early T*b*. Numerous records from the Lower and Middle Eocene of the region. The first recorded appearance in Asia seems to be from Assam (Wilson & Metre 1953), and the last from the Sirki Shales near Kohat, Pakistan (Eames, 1952). Both records are probably correct although neither is supported by figures or descriptions. It occurs commonly in strata of Middle Eocene age in Indonesia. Azzaroli (1952) has reported it from E. Africa in association with *N. fabianii*, a typical T*b* species.

Orbulina. ?Late Upper T*e*. Lower T*f*–Recent. The *Orbulina* datum is so important in Tertiary correlation that it cannot be ignored even in a paper devoted essentially to larger foraminifera. Most planktonic foraminifera cannot be determined readily in random thin sections of limestone but this genus, especially when present in abundance, is an exception.

Records from Lower T*f* are relatively few and are difficult to verify. Some that are believed to be reliable require confirmation. Crespin (1955) reported *Orbulina* from the Tulki and Trealla limestones of Western Australia. Unfortunately, her specimens appear to have been lost. Ludbrook (1961) found *O. universa* and *O. suturalis* in the Pata Limestone of South Australia in association with *Austrotrillina howchini* and *Marginopora vertebralis*, both of which also occur in the Tulki and Trealla limestones, thus suggesting that Crespin's earlier record was accurate. The writer has observed *Orbulina* in association with *Lepidocyclina* (*Nephrolepidina*) spp., *Alveolinella* sp. and *Cycloclypeus* sp. in three samples from New Guinea. In two of these samples the larger foraminifera could be reworked, but in the third (an isolated sample from the Kaifangi River) the association appears to be natural. Although not mentioned by Cole (1963), *Orbulina* is common in the Bonya Limestone of Guam (samples Fi5, Ih5.4, Ts2; personal observation). It also occurs in

* Doubt has recently arisen about the age of the Bukit Asi Limestone. There is a possibility that some of the algae and larger foraminifera in this limestone are reworked. The Palaeocene age quoted by Harlan Johnson (1966. Tertiary Red Algae from Borneo. *Bull. Br. Mus. nat. Hist.* (Geol.) **11**, (6), 257–280, pl. 1–6) now requires confirmation.

the upper part of the Alifan Limestone (sample Ig8). Professor Cole has kindly informed the writer that *Orbulina* was found with a typical T*f* fauna in material from Station 62, Lau, Fiji. This sample is probably Lower T*f* in age.

Van der Vlerk & Wennekers (1929) reported *Orbulina* from an assemblage of typical Upper T*e* larger foraminifera including: *Spiroclypeus, Miogypsinoides dehaarti, Miogypsina, Lepidocyclina mediocolumnata* etc., from Mendingin am Ogen, South Palembang, Sumatra. This record, although unsupported by a figure or description, cannot be disregarded even though it may have been based on a misidentification of *Praeorbulina*. Hanzawa's records (1957) of *Orbulina* in association with *Spiroclypeus* and *Eulepidina* on Saipan are believed to be incorrect. A study of comparable material (U.S.G.S. collections from Saipan in the Smithsonian Institution) failed to reveal this association except in one sample where *Orbulina* was seen together with small (?reworked) fragments of *Eulepidina*. There are numerous other records of the genus in assemblages that would now be regarded as Upper T*e* (e.g., Rutten 1914 : 37), but they are unaccompanied by figures and cannot be verified.

Palaeonummulites incrassatus (de la Harpe). T*b*–Lower T*e*. According to Eames *et al.* (1962), a valuable marker in the Middle East where it occurs throughout the lower part of the Asmari Limestone (= T*d*–Lower T*e*). The same authors also report it from East Africa. The level of its first appearance is difficult to ascertain since there are a number of records of *Nummulites incrassatus* and *N. cf. incrassatus* from the late Middle/Upper Eocene of East Africa and the Middle East (see Silvestri 1942, Bozorgnia 1964 etc.).

Pellatispira. T*b*. The 16 nominal species and varieties are believed to occur entirely within Tertiary *b*. Records of species within Ta_3 are thought to be of an ancestral form which the writer has also seen in Borneo. Although the genus is widespread and very common throughout the region, the ranges of the species are not readily determinable from the literature. *P. orbitoidea* has been reported from the Prang Limestone of Assam along with several species of *Assilina* and *Nummulites* (Nagappa 1956). However, it is not clear whether these genera occur together or separately. If separately, the limestone (400–900 feet thick) should be assigned partly to the Middle and partly to the Upper Eocene. It may be significant that in a later paper Nagappa (1959) made no mention of *Pellatispira* in the Prang Stage. In Europe, the range of *Pellatispira* appears to overlap with those of such typically Middle Eocene genera as *Orbitolites* and *Fasciolites* (Schweighauser 1953), and in Somalia there is an overlap of *Pellatispira* (*P. tudensis*) and *N. fabianii* with *Orbitolites* (Azzaroli 1952). Caudri (1934) reported *Pellatispira* sp. from Ta_2 beds in West Soemba, but her figures are unconvincing. Umbgrove (1928), in his review of the Indo-Pacific members of the genus, said that it occurred in a few rocks with *Assilina*. However, to the best of the writer's knowledge there is no reliable published record of *Pellatispira* in the pre-T*b* rocks of the region.

Peneroplis. ?Ta_1–Recent. Although the genus is widespread, the only well-known fossil species come from the north-western part of the region. Peneroplids are abundant in " back-reef ", miliolid limestone facies in the Middle East and East Africa. Their relative unimportance in the Far East may simply reflect the rarity

of this particular facies in this part of the region. The genus seems to have appeared first in the Palaeocene of East Africa (Banner *et al.* 1967).

Henson (1950) recognized a number of species in strata of Upper Eocene to Middle Miocene age in the Middle East and East Africa. Although he believed that each species has a relatively short range, they appear to overlap and intergrade to such an extent that their reliability as stratigraphical markers is questionable. With one exception, therefore, they are not included on the chart although they are listed below.

P. dusenburyi Henson (?Ta_1–T*b*). *P. evolutus* Henson (Lower T*e*–Lower T*f*). *P. farsensis* Henson. Lower T*f*. Common in Iraq and Iran where it ranges from the Upper Asmari Limestone into the Fars Formation. *P. glynjohnsi* Henson (T*b*–T*d*). *P. thomasi* Henson (T*d*–Upper T*e*).

Praerhapydionina delicata Henson. T*c*–Lower T*e*. Known in Lower Oligocene (T*c*) strata from the western part of the region to the East Indies. Also reported from the Middle and Upper Oligocene (T*d*–Lower T*e*) and Aquitanian (Upper T*e*) parts of the Asmari Limestone by Eames *et al.* (1962).

Sakesaria Davies. Ta_{1-2}. This genus includes several nominal species known from East Africa (Ruggieri 1950), Arabia (Smout 1954, Sander 1962) and Pakistan (Davies & Pinfold 1937). It probably occurs throughout the Upper Palaeocene and is almost certainly present in the Middle Palaeocene; it is unknown above the middle of Ta_2.

Saudia. Ta_1–Ta_2. This genus clearly crosses the Ta_1/Ta_2 boundary, but how far it extends into Ta_2 is unknown. *S. labyrinthica* Grimsdale is supposed to be restricted to beds of Ta_1 age, but so far is known only from the Dunghan Limestone, Pakistan (Khan 1956) and Arabia. However, the validity of the distinction between *S. labyrinthica* and *S. discoidea* Henson (the Ta_2 species) is questionable, and the range of the genus is therefore given here.

Schlumbergerella floresiana (Schlumberger). Pleistocene–Recent. Known only from the East Indies (e.g., Flores Island & Timor). Hanzawa (1952) recognized one species and one variety when he erected the genus.

Somalina Silvestri. Ta_{2-3}. Exact range uncertain ; definitely occurs in the Lower and Middle Eocene of Iraq, and in the ?Lower Eocene of Somalia ; it has recently been found in the lowest beds (conglomeratic limestone) of the Lower Eocene in the Rhaki-Nala section West Pakistan (Bayliss & Samanta : paper in preparation).

Spiroclypeus. ?Ta_3, T*b*–?T*d*. Lower–Upper T*e*. No records from T*c* or T*d* in the Indonesia/West Pacific area.

(a) Eocene species. T*b* in the East Indies, but Azzaroli (1952) figured a specimen (external view only) from the Middle Eocene of Somalia. This could, of course, be a *Heterostegina.* Schweighauser (1953) has reported *Spiroclypeus* from early Upper Eocene and late Lutetian strata in the Mediterranean region.

S. albapustula Cole. T*b*. Pacific Isles (Eniwetok) only. Occurs in the lower part of the T*b* sequence present in drill hole F1.

S. vermicularis Tan. T*b*. Widespread throughout the region. Numerous records, e.g. Cole (1957) Adams (1965). Not known with certainty from basal T*b*.

(b) T*e* species. Although previous range charts for the Far East show the

Oligo-Miocene representatives of this genus making their first appearance at the base of Lower T*e*, the evidence for this is very poor. As mentioned earlier (see under *Heterostegina borneensis*), Leupold & van der Vlerk (1931) recognized that *Spiroclypeus* did not extend to the base of Lower T*e* in Borneo, and recent work on the Melinau Limestone, Sarawak, indicates that it is absent from the lowest T*e* beds in the only section known to be continuous from T*d* to T*e*. The only known post-Eocene species in Europe, *S. blanckenhorni* Henson, is believed by some to range down into the Upper Oligocene of Aquitaine (Butt 1966). However, the nummulites occurring with these spiroclypeids could be reworked, in which case the fauna should be assigned to the Lower Miocene. There is one unsubstantiated report (Thomas 1950) of *Spiroclypeus* from the Middle Oligocene part of the Asmari Limestone.

Pieroni (1965) recorded *Spiroclypeus* from beds of supposed Chattian age in Italy. However, his dating depends on the evolutionary stage reached by the embryonic apparatus of species of *Eulepidina* and *Miogypsinoides*, and these particular evolutionary hypotheses have still to be tested against faunas over which there is good stratigraphical control.

Certain authorities (e.g. Eames *et al.* 1962) have accepted the occurrence of *Spiroclypeus* as proof of a Miocene (i.e., Aquitanian age) for any post-Eocene beds in which it occurs. However, this practice is just as dangerous as determining the age solely on the evolutionary stage reached by the embryonic apparatus of miogypsinids, since it rests on a stratigraphical assumption that has never been proved.

Spiroclypeus has never been proved to occur in natural association with *Nummulites* in the Oligocene of the Indo-Pacific region, although Thomas (1950) said that it was present at the base of the Asmari Limestone in Iran, nor has it been found in beds immediately above those with *Nummulites* except in places where diastems are known to exist. The genus may, therefore, be polyphyletic.

The ranges of the nominal species of *Spiroclypeus* are uncertain*. Differences between species are rather small and they are not easily determinable in random sections.

"Taberina" malabarica (Carter). Lower T*f*. Originally described from the Malabar coast, India, where it occurs in association with *Austrotrillina howchini* (see Adams 1968). The true range of this potentially valuable marker fossil will not be known until the Neogene members of the group to which it belongs (*Archaias s.l.*) have been revised.

Wilfordia sarawakensis Adams. T*b*. A striking species so far reported only from Borneo (Adams 1965), but likely to be recognized elsewhere in the future.

VII. PROBLEMS AND CONCLUSIONS

Outstanding problems

Perhaps the most important contributions that could be made towards improving Indo-Pacific stratigraphical correlation in the near future, would be the detailed description or redescription of the Palaeocene to Oligocene successions in West

* See Postscript p. 128.

Pakistan, the successions in Java on which part of Tan's original work on *Cycloclypeus* was based, the New Guinea Limestone (see Visser & Hermes 1962) and the Kereruan, Taurian and Ivorian limestones of Papua. The Miocene limestones of Ceylon would repay a faunal study, and the Cape Range limestones of Australia need to be re-examined so that Crespin's results can be amplified and her missing specimens replaced. When these successions, and any others that are known to include stage boundaries, have been thoroughly examined, it should be possible to establish the ranges of the most important species of larger foraminifera with considerable accuracy.

As can be seen from Figure 2, carbonate sediments were very well developed in every Letter Stage up to and including Lower T*f*. The absence of Ta_2 limestones in Indonesia is a purely local phenomenon. Upper T*f* and T*g* limestones are, unfortunately, extremely rare even though a considerable period of time was available for their deposition (approximately 8 million years: i.e., Blow's Zones N12–N18). In the Indian region and throughout Indonesia this period was one of intense tectonic activity which resulted in environments unfavourable for the deposition of limestones. It can only be supposed that associated eustatic changes were responsible for the failure of carbonates to be developed on a large scale on what are now the Pacific Islands.

Larger foraminifera are certainly capable of much greater refinement as zone fossils than is practicable at present. However, this is not likely to be achieved until they have been studied in more detail than hitherto, and from sections of considerable thickness. Evolutionary studies could profitably be undertaken in almost any group when material over which there is adequate stratigraphical control becomes available.

Accurate correlation of the sequence of larger foraminifera with the planktonic zonal scheme is, of course, a most important aim, and one which will undoubtedly be realized in the not too distant future.

Conclusions

Contrary to the impression given by previous range charts, very few larger foraminifera can be proved to appear or to disappear at stage boundaries. Where changes of this kind seem to occur, it is because the stages themselves are defined in terms of the ranges of particular genera and species, or because the boundaries in the sections so far described, all coincide with disconformities.

The restriction of some important Tertiary species to Pakistan, Africa or the Middle East, is more apparent than real, and usually reflects the absence of appropriate facies elsewhere in the region. There can be no doubt that facies control is also responsible for the relatively short stratigraphical ranges attributed to some species.

Remarkably little is known about stage boundaries or about the faunas immediately adjacent to them. This is reflected in our inability to establish the ranges of most marker species with any great precision. With a few notable exceptions, transition faunas between the Letter Stages are unknown.

The Oligocene/Miocene boundary appears to coincide approximately with the Lower/Upper T*e* boundary which, in turn, is somewhere within Blow's Zone N4

(= *kugleri* Zone *pars* of Bolli) and a little above the first appearance of the *Globigerinoides quadrilobatus* group of planktonic foraminifera. The *Orbulina* datum must be roughly coincident with the Upper T*e*/T*f* boundary.

Previous authors have invariably placed Lower T*f* in the Lower Miocene. When this is done, practically the whole evolutionary history of " Neogene " (*sensu* T*d*-Recent) larger foraminifera has to be compressed into the late Oligocene and early Miocene, a period of approximately 13 million years. The following 19 million years then has a very low rate of evolution for the same group. With Lower T*f* assigned to the Middle Miocene, as on the present charts, 20 million years are available for the main part of the group's evolutionary history, and the low rate of evolution is confined to the last 12 million years, by which time the majority were already extinct.

It is apparent that the principal value of the Letter Classification is in the recognition and dating of Lower and Middle Tertiary sediments. The late Neogene stages cannot be distinguished satisfactorily on the basis of larger foraminifera and the classification is therefore unsatisfactory for this part of the Tertiary. However, it must be emphasized that European stage names cannot at present be substituted for the Letter Stages, and that a generally acceptable stage terminology for the Tertiary will not be possible until more detailed biostratigraphical work has been done, and the ranges of the larger forminifera correlated more closely with those of the plankton.

POSTSCRIPT

Since this paper went to press an important publication (Cole 1969) on the larger foraminifera from two drill holes on Midway Atoll, has appeared. Apart from extending the geographical ranges of some important Indo-West Pacific species a little farther to the east, Cole's paper contains the following information relevant to the present work :

1. A Tertiary *e* (Upper T*e* in the writer's opinion) fauna is recorded from a depth of 590–1,126 feet in the Reef hole. It includes *Austrotrillina striata* Todd & Post, *Flosculinella globulosa* Rutten, *Marginopora vertebralis* Blainville, *Miogypsinoides dehaarti* (van der Vlerk) and *Spiroclypeus margaritatus* (Schlumberger).

2. The fauna in the beds between the surface and 590 feet includes *Borelis pulchrus* (d'Orbigny) [called *B. melo* (Fichtel & Moll) by Cole], *Heterostegina suborbicularis* d'Orbigny, *Marginopora vertebralis*, *Sorites marginalis* (Lamarck), and *Sorites orbiculus* (Forskål). This assemblage could be of any age from Middle Miocene to Recent, but the total absence of diagnostic Lower and Upper T*f* species suggests that a large part of Miocene time is not represented in these holes.

3. *Marginopora vertebralis* occurs in beds that are certainly dateable as Tertiary *e*, thus confirming that the range quoted in this paper is correct.

Cole attempts to show that all the Miocene species of *Spiroclypeus* in the Pacific region can be assigned to *S. margaritatus*, that *Miogypsinoides bantamensis* Tan and various other " species " are synonyms of *M. dehaarti*, and that *Borelis melo* is a senior synonym of *B. pygmaeus* and *B. schlumbergeri*. While acknowledging that there are too many nominal species in each of these genera, the present writer believes that Cole has stretched the available evidence too far and has obscured the stratigraphical value of some important species.

THE RANGES OF SOME FORAMINIFERA IN THE INDO-WEST PACIFIC REGION

FIG 3

FIG. 3. The stratigraphical distribution of some important marker foraminifera in the Indo-West Pacific region.

This chart should be used in conjunction with the text (pp. 109–126).

Solid lines = proven range.

Broken lines = range uncertain but valid records occur within these limits.

? = record(s) of doubtful validity.

* = no records as yet, but the genus known to range down into this stage in the Mediterranean region.

The ranges of genera such as *Cycloclypeus* and *Nummulites* are not shown since they are fully covered by those of the listed species. Genera known to range right through the Tertiary have also been omitted.

ALPHABETICAL LIST OF GENERA AND SPECIES

	Position on chart
Actinosiphon punjabensis Davies	6
Aktinocyclina spp.	30
Alveolinella fennemai (Checchia-Rispoli)	106
Alveolinella quoyi d'Orbigny	112
Archaias operculiniformis Henson	68
Archaias vandervlerki de Neve	77
Assilina spp.	16
Assilina dandotica Davies	15
Assilina exponens (Sowerby)	23
Assilina granulosa (d'Archiac)	17
Assilina spira (de Roissy)	35
Asterocyclina spp.	29
Asterorotalia pulchella (d'Orbigny) gr.	114
Austrotrillina asmariensis Adams	63
Austrotrillina howchini (Schlumberger)	93
Austrotrillina paucialveolata Grimsdale	66
Austrotrillina striata Todd & Post	72
Baculogypsina sphaerulata (Parker & Jones)	116
Biplanispira spp.	43
Borelis melo curdica Reichel	102
Borelis melo melo (Fichtel & Moll)	99
Borelis pulchrus (d'Orbigny)	118
Borelis pygmaeus Hanzawa	51
Borelis schlumbergeri (Reichel)	113
Boreloides eniwetokensis Cole	54
Bullalveolina bulloides (d'Orbigny) emend. Reichel	70
Calcarina spengleri (Linné)	115
Chapmanina spp.	42
Coskinolina rotaliformis Cole	55
Cycloclypeus carpenteri Brady	111
Cycloclypeus eidae Tan	76
Cycloclypeus indopacificus Tan	96
Cycloclypeus koolhoveni Tan	62
Cycloclypeus oppenoorthi Tan	65
Cycloclypeus posteidae Tan	92
Cycloclypeus (*Katacycloclypeus*) *annulatus* Martin	101
Cycloclypeus (*Radiocycloclypeus*) *radiatus/stellatus* Tan	108
Dictyoconoides flemingi Davies	9

(*continued overleaf*)

(Caption to Fig. 3 (contd.))

	Position on chart
Dictyoconoides cooki (Carter)	22
Dictyoconus melinauensis Adams	61
Discocyclina archiaci (Schlumberger)	44
Discocyclina dispansa (Sowerby)	25
Discocyclina javana (Verbeek)	33
Discocyclina omphalus (Fritsch)	39
Discocyclina ranikotensis Davies	13
Discocyclina sella (d'Archiac)	40
Discocyclina sowerbyi Nuttall	26
Discocyclina undulata Nuttall	28
Fabiania spp.	32
Fasciolites spp.	7
Flosculinella bontangensis (Rutten)	98
Flosculinella globulosa (Rutten)	84
Flosculinella reicheli Mohler	83
Gypsina marianensis Hanzawa	90
Halkyardia spp.	31
Heterostegina bantamensis Tan	60
Heterostegina borneensis van der Vlerk	75
Heterostegina saipanensis Cole	47
Lacazinella reicheli Bursch	52
Lacazinella wichmanni (Schlumberger)	38
Lepidocyclina (*Eulepidina*) spp.	64
Lepidocyclina (*Nephrolepidina*) spp.	69
Lepidocyclina (*N.*) *ferreroi* Provale	100
Lepidocyclina (*N.*) *inflata* Provale	87
Lepidocyclina (*N.*) *isolepidinoides* van der Vlerk	67
Lepidocyclina (*N.*) *japonica* (Yabe)	88
Lepidocyclina (*N.*) *martini* (Schlumberger)	95
Lepidocyclina (*N.*) *parva* Oppenoorth	71
Lepidocyclina (*N.*) *sumatrensis* (Brady) & vars.	79
Lepidocyclina (*N.*) *verbeeki* (Newton & Holland)	89
Lepidocyclina (*Tribliolepidina*) *orientalis* van der Vlerk	109
Lepidocyclina (*T.*) *radiata* Martin	105
Lepidocyclina (*T.*) *rutteni* van der Vlerk	107
Lepidocyclina flexuosa Rutten	86
Lepidocyclina acuta (Rutten)	87
Lepidocyclina talahabensis van der Vlerk	110
Linderina spp.	21
Lockhartia spp.	4
Marginopora vertebralis Blainville	94
Meandropsina anahensis Henson	81
Miogypsina spp.	80
Miogypsina thecideaeformis (Rutten)	85
Miogypsinoides spp.	73
Miogypsinoides bantamensis Tan	78
Miogypsinoides complanatus (Schlumberger)	74
Miogypsinoides cupulaeformis (Zuffardi-Comerci)	91
Miogypsinoides dehaarti van der Vlerk	82
Miscellanaea miscella (d'Archiac & Haime)	1
Nummulites atacicus Leymerie	18
Nummulites carteri d'Archiac & Haime	34

(Caption to Fig. 3 (contd.))

	Position on chart
Nummulites chavannesi de la Harpe	45
Nummulites fabianii (Prever)	46
Nummulites fichteli Michelotti	58
Nummulites gizehensis (Forskål)	27
Nummulites javanus Verbeek	24
Nummulites millecaput Boubée	37
Nummulites nuttalli Davies	11
Nummulites pengaronensis Verbeek	36
Nummulites thalicus Davies	10
Nummulites vascus Joly & Leymerie	57
Operculina canalifera d'Archiac	2
Operculina sindensis Davies	12
Operculina salsa Davies	3
Opertorbitolites spp.	8
Orbitolites complanatus Lamarck	19
Orbulina spp.	97
Palaeonummulites incrassatus (de la Harpe)	53
Pellatispira spp.	41
Peneroplis farsensis Henson	104
Praerhapydionina delicata Henson	59
Sakesaria spp.	5
Saudia spp.	14
Schlumbergerella floresiana (Schlumberger)	117
Somalina spp.	20
Spircolypeus spp.	48
Spircolypeus albapustula Cole	50
Spiroclypeus vermicularis Tan	49
Taberina malabarica (Carter)	103
Wilfordia sarawakensis Adams	56

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Printed in Great Britain by
Alden & Mowbray Ltd
at the Alden Press, Oxford

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L. R. M. COCKS

BULLETIN OF
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GEOLOGY Vol. 19 No. 4
LONDON: 1970

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- 6 NOV 1970
NATURAL HISTORY

BY
LEONARD ROBERT MORRISON COCKS

Pp. 139–203 ; 17 *Plates* ; 9 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 19 No. 4
LONDON 1970

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World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.).

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 3 *November*, 1970 *Price* £5·10

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By L. R. M. COCKS

CONTENTS

		Page
I.	Introduction	142
II.	History of previous research	143
III.	Morphological terminology	144
IV.	Functional morphology	146
V.	Ecology	152
VI.	Systematic palaeontology	154
	Superfamily Plectambonitacea Jones	154
	Family Leptellinidae Ulrich & Cooper	155
	Subfamily Leptellininae Ulrich & Cooper	155
	Merciella Lamont & Gilbert	155
	Merciella vesper Lamont & Gilbert	155
	leptellininid gen. et sp. indet.	155
	Subfamily Leptestiininae Havlíček	156
	Leangella Öpik	156
	Leangella triangularis (Holtedahl)	158
	Leangella scissa (Davidson)	158
	Leangella segmentum (Lindström)	162
	Family Sowerbyellidae Öpik	164
	Subfamily Sowerbyellinae Öpik	164
	Eoplectodonta Kozlowski	166
	Eoplectodonta duplicata (J. de C. Sowerby)	169
	Eoplectodonta penkillensis (Reed)	172
	Eoplectodonta transversalis (Wahlenberg)	177
	Eoplectodonta duvalii (Davidson)	182
	Ygerodiscus Havlíček	184
	Ygerodiscus undulatus (Salter)	185
	? *Ygerodiscus cornutus* (Davidson)	188
	Anisopleurella Cooper	189
	Anisopleurella gracilis (Jones)	189
	Subfamily Aegiromeninae Havlíček	191
	Aegiromena Havlíček	191
	? *Aegiromena* sp.	191
	Chonetoidea Jones	192
	Chonetoidea papillosa (Reed)	193
	Aegiria Öpik	195
	Aegiria garthensis (Jones)	195
	Aegiria grayi (Davidson)	197
VII.	Acknowledgments	199
VIII.	References	199

SYNOPSIS

Silurian plectambonitacean brachiopods are reviewed, and the number of British species reduced from twenty-three to eleven. Swedish and Bohemian forms are also considered, and the much quoted species *Eoplectodonta transversalis* (Wahlenberg 1819) and *Leangella segmentum* [Angelin MS] (Lindström 1861) are revised ; it is found that *E. transversalis* is confined to the Lower Visby Marl (uppermost Llandovery) of Gotland, and that the common Wenlock species of Britain and Sweden is *E. duvalii* (Davidson 1847). Most Silurian plectambonitaceans are extremely variable in shape and size.

The morphology and function of *Eoplectodonta* and *Leangella* are discussed, and the articulation and muscle systems described. It is postulated that when *Eoplectodonta* was being overturned, it could flap its valves, sending out water jets enabling it to right itself. It may also have achieved its water circulation by opening and closing its valves, a more efficient method than a ciliary beat in such a thin inter-valve space. The ecology is also considered, *Eoplectodonta*, *Ygerodiscus* and *Leangella* lived concave upwards free on the sea floor ; *Aegiria* lived an attached life, probably to algae. All the Silurian genera of the Plectambonitacea are most common in the deeper-water *Clorinda* Community.

I. INTRODUCTION

THIS paper continues the study of Silurian strophomenide brachiopods. The scope has widened ; the first paper, on the strophеodontids (Cocks 1967), dealt only with the Llandovery of the Welsh Borderland, the second, on the strophomenids (Cocks 1968), covered the Llandovery of Britain. The present paper includes at least a review of all the species so far described from the Silurian of Europe.

One of the reasons for the increase in age range is that the plectambonitaceans found in the Upper Silurian, i.e. the Wenlock and Ludlow Series, are on the whole lingering members of genera common in the Llandovery. Indeed, after the appearance of *Ygerodiscus* at the end of the Lower Llandovery, no new genera of plectambonitaceans appeared in Europe until the very close of the Silurian.

The acme of the Plectambonitacea was in the Middle Ordovician, after an explosive radiation in the upper part of the Lower Ordovician. Of the six families and twelve subfamilies in the Treatise on Invertebrate Paleontology (Williams 1965), whose classification is followed here, only two families and four subfamilies have representatives in the Silurian, although individual species may be very abundant. Their ecological niches were occupied first by small strophеodontids, such as *Pholidostrophia* and then later by the chonetids, and the whole of the superfamily Plectambonitacea was extinct by the beginning of the Upper Devonian.

No-one appears to have appreciated the extreme variability of Silurian plectambonitaceans in exterior shell proportions and in the varied development of internal structures, both as adults and during ontogeny. A large number of names have been erected in the past for forms within the limits of each other's variability ; hence the many taxa put into synonomy in this paper. No new species or genera have been erected.

The Plectambonitacea possess a very different morphology from any living brachiopod, and their possible mode of life is discussed.

New stages have recently been erected within the Llandovery Series (Cocks, Toghill & Ziegler, 1970), in ascending order Rhuddanian, Idwian, Fronian and Telychian, and these names are used in this paper.

II. HISTORY OF PREVIOUS RESEARCH

During the nineteenth century, Silurian species of plectambonitaceans were described by J. de C. Sowerby, Davidson and Salter in Britain, and by Wahlenberg, Shaler, Barrande and Lindström abroad. Most were allotted to the genus *Leptaena*, to which Dalman (1828) had referred the first described species, Wahlenberg's *Anomites transversalis*. Not until a paper by Reed appeared in 1917 were satisfactory descriptions published ; however his work was confined to the Girvan district of Scotland.

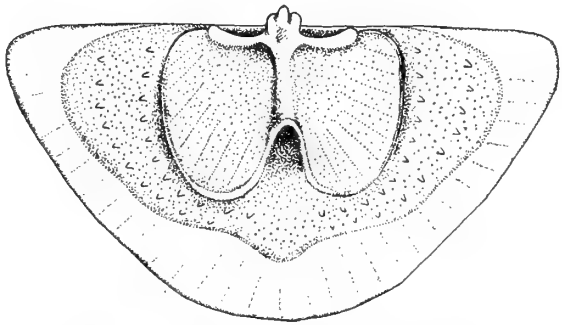

FIG. 1. Brachial valve of *Leangella scissa*.

The only major paper on British Silurian plectambonitaceans is that by O. T. Jones (1928), whose interest in the group was aroused at the turn of the century when working for the Geological Survey. In Pembrokeshire and Carmarthenshire the Ordovician and Silurian rocks consist mainly of rather similar mudstones, and Jones recognised a succession of plectambonitacean faunas in the Llandeilo, Bala and Llandovery rocks, which he was able to use in mapping (Jones *in* Strahan *et al.* 1914 ; Cantrill *et al.* 1916).

Subsequently (1928), he described three new genera of plectambonitaceans, *Sowerbyella*, *Leptelloidea* and *Chonetoidea*, with twelve new species and six new " varieties " of which seven species and four " varieties " are from the Lower Silurian, chiefly of Pembrokeshire.

There followed Kozlowski's great work (1929) on the Silurian (now mostly Lower Devonian) of Podolia, then in Poland, now in Russia. He separated those sowerbyellids with denticles into a new genus, *Plectodonta* ; and, as its inferred predecessor, the partly denticulate sub-genus *Eoplectodonta* (with as type one of Jones's Welsh species, *Sowerbyella precursor*). Soon afterwards, Öpik, working on Baltic material (1932, 1933), clarified the familial divisions within the plectambonitaceans, and, although dealing mainly with Ordovician forms, divided Jones's genus *Chonetoidea* into *Chonetoidea* and *Aegiria*, and *Leptelloidea* into *Leptelloidea* and *Leangella*. Öpik's elucidation of plectambonitacean morphology represented a great advance.

Since then there has been no published work on British Silurian species, apart from a paper by Lamont & Gilbert (1945) in which the rare genus *Merciella* was named. Abroad, a few species have been described, as an incidental part of larger faunal

studies, but the only major contributor has been Havlíček (1952, 1961, 1967) with detailed studies on the Bohemian fauna. However much knowledge has been gained on Ordovician forms, particularly by Cooper (1956) and Williams (1962 etc.), and an acceptable classification has been formulated (Williams 1965).

III. MORPHOLOGICAL TERMINOLOGY

In most descriptions of the superfamily, the morphological terminology used has been based on the assumed function of the structures, although the Plectambonitacea are among those brachiopods in which direct homology with living forms is most conjectural. Thus a descriptive terminology is defined and used in this paper without functional connotation ; the attempt is made subsequently to assess the use of the structures in the live animal. There is a shortage of terms which do not connote some degree of function, and it has been necessary to create two new terms, bema and clavicular plates.

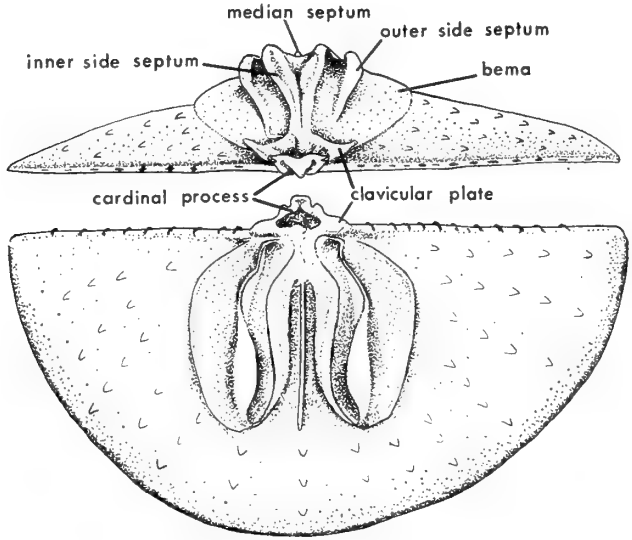

FIG. 2. Brachial valve of *Eoplectodonta duvalii*.

The term " anderidium " (Sadlick 1965) was defined primarily for the chonetids (according to its original definition it replaces the term " lateral septa " as used by Muir-Wood, 1962, fig. 3A). Sadlick refers to the " anderidia " of sowerbyellids, but he does not elaborate on this use, or provide or refer to illustrations. Thus it is not clear which structures he had in mind for sowerbyellids, and whether these would be homologous with the anderidia in chonetids, and so the term is not used in this paper.

Gill (1969), whilst describing the Notanopliidae, an interesting Devonian group which might have been descended from some sowerbyellid, erected a new series of names for various sets of septa in both valves. He rightly draws distinctions be-

tween the different functions of the sets of septa, but he draws these distinctions before giving them their names. If the organ were to be interpreted differently by any subsequent worker, then the name would need changing, i.e. it is again a subjective system, and has not been used in this paper. Gill also restricts the use of the terms ventral median septum (which he calls " venmidseptum ") and dorsal median septum (which he calls " dormidseptum ") to structures which commence at the hinge line. Since the meaning of septum is " something which encloses something " (and has been used in brachiopod morphology for many years as meaning some sort of small wall, usually radial, inside any part of a brachiopod valve), and " median " is also unambiguous, it seems a pity to restrict the meaning of this useful term to structures which reach the hinge line ; for this reason Gill's restriction of the terms is not followed.

Another feature often seen inside plectambonitacean brachial valves is a depression bounded posteriorly by the cardinal process, postero-laterally by the socket plates and anteriorly by the median high septal field. Some authors have named this depression ; Öpik (1933) called it the " Schlossgrube " and Muir-Wood (1962) the " alveolus ". However it can be misleading to use positive terms for negative features, and I prefer to think of this space as a gap between structures, rather than as a structure in its own right, and so a special name is not used in this paper.

There follows a glossary of some of the morphological terms used in this paper for the two families, together with the equivalents of previous workers (Jones 1928, Kozlowski 1929, Öpik 1933, Williams 1965 and Havlíček 1967). Other terms used will be found in the Treatise on Invertebrate Paleontology (Williams *et al.* 1965).

LEPTELLINIDAE

Central shaft and **lateral processes** of cardinal process : the cardinal process is trifid, with a central shaft and two, or sometimes four, lateral processes (Jones : cardinal process, Öpik : Mittelzapfen des Schlossfortzatzes und seitlichen Zapfens, Williams : cardinal process and subsidiary ridges).

Dental Plates : pair of structures supporting the teeth, between them and the floor of the pedicle valve (Jones : dental lamallae, Williams : dental plates).

Platform : raised area of secondary shell in the brachial valve upon which striae are often seen (Jones : visceral disc, Öpik : Brachiallamellen, Williams : lophophore platform, Havlíček : visceral platform).

Socket Plates : pair of structures forming the anterior support in the brachial valve for the pedicle valve teeth (Jones : crural bases, Williams : socket ridges, Havlíček : brachiophores).

Subperipheral rim : ridge running round either valve subparallel with the anterior commisure which curves round posteriorly to merge with the hinge line or the bases of the socket plates (Jones : concentric elevation, Öpik : Diaphragma (in brachial valve), Akkomodationspur des Diaphragmas (in pedicle valve), Williams : subperipheral rim, Havlíček : diaphragm (in brachial valve), submarginal ridge (in pedicle valve)).

SOWERBYELLIDAE

Bema (new term, from Greek βῆμα meaning a platform) : platform of secondary shell in the central field of the brachial valve, its function is discussed below. A new term is coined since it is debateable whether this organ is homologous with the platform of the Leptellinidae. It is certainly different in structure, hence a new objective term with no functional connotation (Kozlowski : branche externe de la lamelle brachiale, Öpik : Brachiallamellen, Williams : lophophore platform, Havlíček : peripheral rim of visceral field).

Clavicular plates (new term from Latin *clavis*, meaning a key) : pair of structures projecting antero-laterally from the cardinal process ; their function is discussed below (Kozlowski : plaques crurales, Öpik : Cruralzähnen, Williams : socket ridges).

Fossettes : a series of small pits along the hinge line into which the denticles of the opposite valve fit (Kozlowski : fossettes denticulaires).

Inner side septa : the pair of septa in the brachial valve which lie immediately laterally of the median septum (Jones : submedian septa, Kozlowski : branche interne de la lamelle brachiale, Öpik : Seitensepten, Williams : submedian septa).

Outer side septa : the pair of septa in the brachial valve which lie outside the inner side septa (Jones : transverse septa, Kozlowski : lamelle brachiale intralobaire, Öpik : Seitensepten, Williams : divergent ridges).

IV. FUNCTIONAL MORPHOLOGY

No living brachiopod has a form similar to the Plectambonitacea. The extreme thinness of a plectambonitacean (when its valves were together) in relation to its valve area, and in addition its curved shape, often more than a semicircle in cross-section, make comparison with living brachiopods impossible in all but the most general way ; the terebratulides, rhynchonellides and thecideaceans all have a relatively large internal cavity in proportion to their valve size.

In this section attention will be confined to the two most common Silurian plectambonitacean genera, *Leangella* and *Eoplectodonta*. The other genera described in this paper are presumed to have functioned in a similar way to these two genera, except *Chonetoidea* and its close relative *Aegiria*, which differ in having a functional pedicle.

The articulation system, the muscle system, the water circulation-feeding system and the mantle canal system will be considered in turn.

Articulation.

The Ordovician *Sowerbyella* had a simple articulation consisting of a pair of teeth in the pedicle valve which fitted into the brachial valve between the hinge line and a pair of socket plates (both well figured in *Sowerbyella nasuta* by Cooper, 1956, pl. 199). Both these structures occur in the earliest, Middle Ordovician, species of *Eoplectodonta* in which Cooper described small teeth as well as socket plates (1956 : 808, also pl. 208). They also possess denticles on the pedicle valve hinge line with corresponding fossettes in the brachial valve, one of the primary diagnostic features of *Eoplectodonta*.

Incidentally there is no correlation between the proportion of the hinge line covered by denticles and the geological age of the species, as supposed by Kozlowski (1929) when he erected *Eoplectodonta*. Smaller teeth are still present in some Ashgill species. However by early Silurian time none of the species of *Eoplectodonta* had teeth ; presumably articulation was achieved by the system of denticles and fossettes on the hinge line. However they all possessed well developed " socket plates " in the brachial valve. Since these " socket plates " could not have performed their named function in those Silurian species without teeth, the term " clavicular plates " has

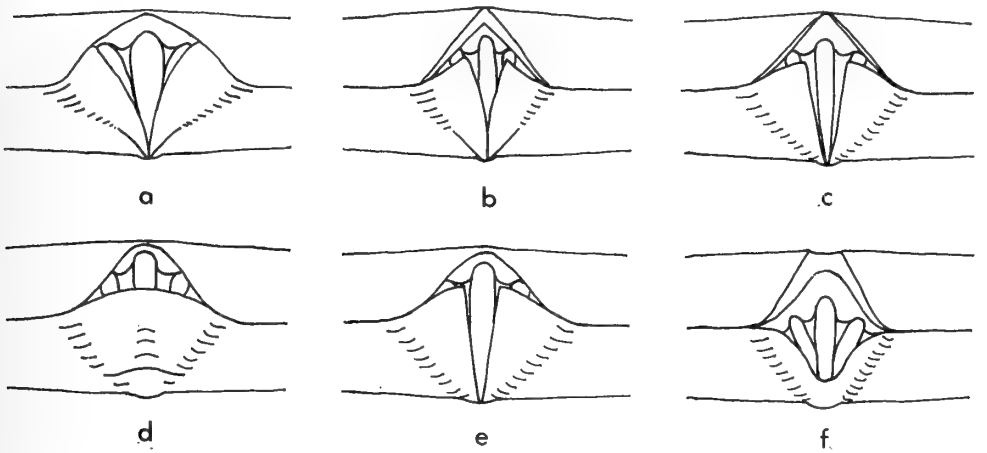

FIG. 3. Interareas of *Eoplectodonta* (a–e) and *Plectodonta* (f), pedicle valve above, brachial valve below. (a) *E. duplicata* (from BB 31738, Lower Llandovery, Gasworks Mudstone, Wales) with open delthyrium and chilidial plates, behind them the central shaft and lateral processes of the cardinal process. (b) *E. penkillensis* (from BB 31840, Upper Llandovery, Hughley Shales, England) showing blade-like deltidial plates and chilidial plates. (c) *E. transversalis* (from BB 32422 Upper Llandovery, Lower Visby Marl, Sweden) showing chilidial plates and very small deltidial plates. (d) and (e) *E. duvalii* from the same locality (both registered B 1587 from Lower Wenlock, Buildwas Beds, England) both with open delthyrium, but one specimen with entire chilidium and the other with discrete pair of chilidial plates. (f) *Plectodonta mariae* (from B 81377, Lower Devonian, Borschov Beds, U.S.S.R.) showing deltidium and low but entire chilidium. What these diagrams do not convey is the relative angles of the interareas of the two valves, which are sometimes great, for example in *E. duvalii* ; however the interareas of *P. mariae* are set in nearly the same plane.

been used in this paper for these structures. These clavicular plates grew in the same way as the socket plates of the Ordovician species with teeth, but the fact of their continued existence after the teeth had vanished from the stock, argues that the clavicular plates must have had some function in addition to their now obsolete role as socket plates. Havlíček, without discussion, describes the clavicular plates as brachiophores. However there is no direct evidence for this function, which is why an objective term has been coined here for the plates. It is possible that they might

have functioned as brachiophores, giving some sort of rigid support to the ends of the lophophores ; on the other hand they may simply have given some support to some organ within the coelome.

In contrast, the teeth and socket plates of *Leangella* remained until its extinction.

The muscle system.

The diductor muscle system of *Eoplectodonta* consisted of a pair of muscles running from the small scars on each side of the short median septum in the umbo of the pedicle valve to the pair of furrows at the top of the prominent cardinal process. The adductor muscle system is open to more varied interpretation. In the pedicle valve there is a very large pair of diamond-shaped scars in the umbonal region (Plate 6, figs. 1, 2, 7–9), but in the brachial valve there is no obvious site for muscle attachment (Plate 5, figs. 3–12). The oval areas to be seen on the specimens figured on Plate 5, figs. 3 and 6 and Plate 6, figs. 4 and 5, in the antero-median area of the brachial valves, are present between the median septa and inner side septa in only a very few valves from the Gasworks Mudstone, and may represent areas from which mantle tissue had been worn during adult life by contact with the pedicle valve when the valves were shut. In any case, the fact that these areas are absent from nearly all brachial valves precludes their choice as a probable attachment site for the adductor scars. The adductor muscles were probably attached in the brachial valve to the outer sides of the outer side septa and onto the bema, between its lateral edges and the outer side septa, since they are opposite the scars in the pedicle valve. Considering the antero-lateral splaying of the pedicle valve adductor scars and the shape of both valves, that general area of the brachial valve would be the most likely place for the attachment of the adductor muscles on mechanical grounds.

In *Leangella* the system is more certain. The diductor muscles went from the small lanceolate scars in the pedicle valve umbo to the cardinal process, in a similar way to *Eoplectodonta*. The adductor muscles ran from the umbonal muscle field in the pedicle valve, which was raised up off the valve floor to form a platform, to the muscle platform in the brachial valve. On both valves the attachment striae are clearly visible (Plate 1, fig. 12 for pedicle valve and Plate 4, figs. 9 and 10 for the brachial valve).

Thus in both *Eoplectodonta* and *Leangella* there was a notably strong muscle system. The reasons for this will now be considered.

As adduced in the section on ecology below, plectambonitaceans must have lived concave upwards. On the other hand, such a position is not as hydrodynamically stable as convex upwards, and when any sort of severe current or wave action occurred then the brachiopod would have been overturned and killed, particularly as its pedicle was apparently non-functional in adults. As a result, the Plectambonitacea may well have evolved to increase the strength of their muscle system so that individuals could right themselves by a series of snapping actions whilst they were in process of being overturned. *Eoplectodonta* also possesses a septal system which is tubular (in cross-section parallel to the hinge line). When the water was expelled quickly from inside the brachiopods by quick action of the adductor muscles, these tubes would have directed much of the water anteriorly in jets, a far more effective

righting mechanism than an indiscriminate expulsion of water equally round the gape. This power of self-righting would obviously have had a high survival advantage. How these brachiopods may have used this strong muscle system in a secondary role is discussed below.

Water Circulation and Feeding System.

All modern articulate brachiopods feed by creating a current of water from the beating of the cilia on their lophophores, and then by straining the food from the water as it swirls between the two valves. The straining is achieved by the separation of the space between the valves into two compartments, for water before and after it has been strained (Rudwick 1962). As a result, various fairly rigid lophophore systems, often with calcareous supports, have evolved, adapted to the dual function of creating a ciliary beat for water circulation and of straining the particles from the water and passing them to the mouth.

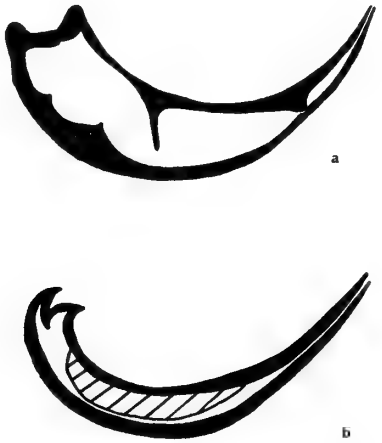

FIG. 4. Cross-section through the median plane of (a) *Leangella* and (b) *Eoplectodonta*. The shaded area in *Eoplectodonta* shows the profile of one of the inner side septa.

Eoplectodonta, and by inference other plectambonitaceans, may have accomplished the water circulation in a different way. As seen above, the animals had a powerful muscle system. The simple action of opening or closing their valves would have caused a very large increase in the volume of water inside the shell. An opening of about ten degrees would cause the shell to hold about four times as much water as when the valves were shut. As the valves opened, a large quantity of water would have come in, with the largest part of the volume in the central part of the shell, where the gape would be at its maximum. In cross-section parallel to the hinge line the spaces between the inner and outer septa are tubular anteriorly, and widen out again posteriorly. This arrangement would help to channel the incoming or outgoing water to make the system more controlled. Another feature which improved

the water circulation is the increased valve length. For about their anterior third, adult valves grew more or less parallel to each other (Text-fig. 4), so that when the valves were shut the whole of that sector of the valves were very close together, and that when the valves opened there would have been a faster and more forceful inrush of water than if the extra valve length had not been there. However, this latter advantage may have been partially offset by the increased weight of the added calcification, and the extra anterior valve length may simply have been to keep the commissural feeding gape higher off the substrate.

This system of water circulation would obviate the need for a ciliary beat circulation system, and the latter could even have atrophied, possibly in the stock as a whole some time during the Ordovician, or possibly in each individual soon after the larval stage. The lophophore would then be relegated into a role solely concerned with the collection of food. The septal tubes and general valve morphology would channel the water right up near the mouth of the animal, and the lophophore could either have degenerated into a small filtering device just round the mouth area, or it could have remained as a larger structure perhaps adhering to the septa or floor of the bema. On the other hand, a weak ciliary beat could have continued through life, so as to help control the filtering, and as a means of rejection of unwanted particles.

In *Leangella* a similar system might have operated. Here the subperipheral rim in the brachial valve and its interlocking counterpart in the pedicle valve (Text-fig. 4b) provides the narrow point through which the water would have rushed through quickly when the valves opened. In *L. scissa* (Plate 2, fig. 4) the anterior part of the subperipheral rim was curved in such a fashion as to direct the incoming or outgoing water centrally up the valve. In *Leangella*, as may be seen from the striae, the muscle system occupied all of the platform area, and the lophophore was presumably arranged in the area between the muscle platform and the subperipheral rim.

In both *Eoplectodonta* and *Leangella* the papillae are markedly coarser, but less numerous, in the brachial valve as opposed to the pedicle valve. It is possible that this arrangement provided a better attachment surface in the brachial valve for the mantle, since that valve would have been in motion for a much greater part of the time than the largely sessile pedicle valve.

No living brachiopod achieves its water circulation by the valve movement method postulated above. However the same idea has been put forward for another extinct group of strophomenides, the Richthofenacea. Rudwick (1961) has advanced the theory that these rather aberrant, coral-shaped brachiopods circulated their water by flapping their lid-like brachial valves ; but the morphology of the Richthofenacea is even further removed from that of a conventional brachiopod than that of the Plectambonitacea.

The Mantle Canal System.

There is some variation seen in the mantle canal patterns of the pedicle valve of *Eoplectodonta* (Text-fig. 5). The *vascula media* are prominent, although the *vascula genitalia* and gonadal sac area illustrated by Williams (1965 : H131) for *Sowerbyella* have not been seen.

In nearly all specimens of *Eoplectodonta* the mantle canals are well impressed in the pedicle valve, whilst in the brachial valve there is usually no trace of them, even allowing for the fact that the edge of the main body coelome would have come further anteriorly in the brachial valve than in the pedicle valve. A possible reason for this discrepancy (if it is real rather than apparent) follows from the interpretation of the muscle and water circulation systems discussed above. Since the anterior parts of the two valves were more or less parallel to each other (Text-fig. 4), the setae at the ends of the vascular system would also have been more or less parallel, assuming, that is, that the setal direction in plectambonitaceans was similar to that of modern brachiopods, in the same plane as valve growth (as illustrated by Williams 1965 : H82). If they were parallel, then the functions of the setae in the two valves

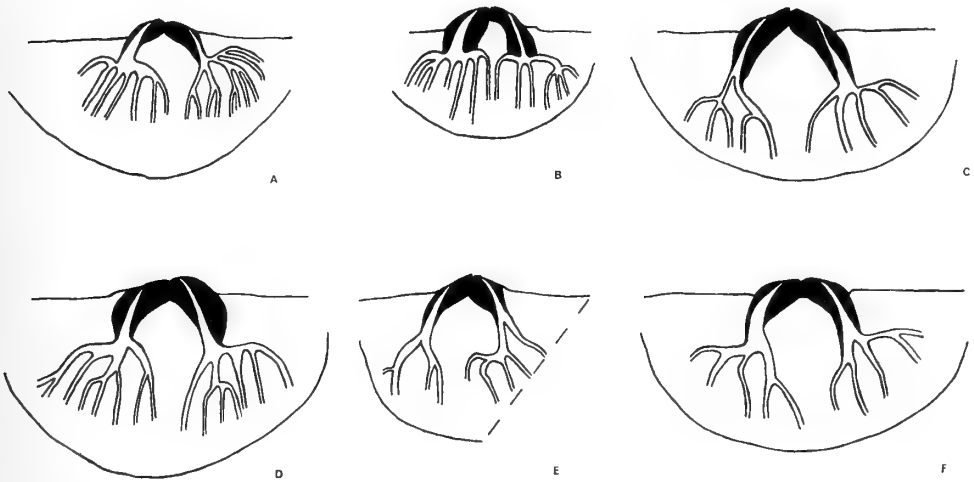

FIG. 5. Mantle canal patterns in the pedicle valve of *Eoplectodonta duplicata*. The figures are drawn as internal moulds and the adductor muscle scars coloured black. (a) from BB 31990 (Plate 8, figs. 3, 4), Woodland Point, Girvan, (b) from GSM 37579, Plate 8, fig. 7), Gasworks Sandstone, Union Hill, Pembrokeshire. (c) to (f) all from Gasworks Mudstone, the Gasworks, Haverfordwest, Pembrokeshire (c) BB 31753 (Plate 6, fig. 8), (d) and (e) both BB 31732 (Plate 6, fig. 3), (f) BB 31740 (Plate 6, fig. 7).

would have been to some degree duplicatory. Since the brachial valve would have been in motion much more than the pedicle valve, it would obviously have preferred to lighten its load as much as possible. For these reasons, the setae, and the corresponding mantle canals, could have become enlarged in the pedicle valve as compared with the brachial valve.

However there is no suggestion that the setae and vascular system became atrophied in the brachial valve ; there are rare specimens of *Eoplectodonta* (for example the individual figured in Plate 5, figs. 3 and 6) in which the mantle canal

system is clearly visible, starting as two trunks (presumably the *vascula myaria*) at the anterior end of the bema, and radiating in a manner similar to that of the pedicle valve.

V. ECOLOGY

The autecology of the animals will be considered first, followed by the synecology.

Leangella, *Eoplectodonta* and *Ygerodiscus* (and also probably *Merciella* and *Anisopleurella*, but there is too little material to be sure) were presumably benthic forms. Their pedicles were wholly or partly atrophied during adult life, and they lay free on the sea floor. The only stable positions for shells of highly curved shape is with the diameter of the valve semicircle lying parallel with the sea bed. This gives a choice of two positions, with pedicle valve on top or with pedicle valve underneath. As argued by Williams (1953 : 33) for the stropheodontids, brachiopods derive their food from circulating sea water, and this could only have entered through the gap between the two valves. If the pedicle valve was uppermost, it follows that this gap would have been buried in the sea floor, an impossible condition for the circulation of water. Thus these genera must have lived with their pedicle valve downwards on the substrate, which they appear to have preferred to be soft. As argued in the section on functional morphology above, they probably also had the power to right themselves if tipped off balance, by a quick muscular snapping action. On death, however, they would have been easily upturned by currents into the hydrodynamically more stable position, i.e. pedicle valve on top, in which they are very often found fossil.

Havlíček (1967) and Bergström (1968) have demonstrated the case for an epiplanktonic existence for some plectambonitacean genera, in particular *Chonetoidea*. Both these authors figured strings of valves in apparent life association, and also associated, in Bergström's case, with dark, presumably organic, patches which may have been algal in origin. In the Silurian *Aegiria* is sometimes found in the same way occurring occasionally in rocks in which the other benthic fauna is restricted, suggesting adverse conditions. However *Aegiria* also occurs in ones and twos as an apparently normal constituent of the *Clorinda* Community. There is no appreciable difference in the morphology of *Aegiria* in these two forms of occurrence. All *Aegiria* have a foramen big enough to contain a pedicle which was presumably functional, and a possible way to reconcile the two types of occurrence is to postulate that *Aegiria* normally lived an attached life, perhaps to brown or red algae, at *Clorinda* Community depth. From time to time strands of algae were uprooted, and transported, together with the attached *Aegiria*, into environments which were inimical to brachiopods, at times even euxinic. The brachiopods attached to the algae thus drifted further than the other brachiopod genera which lay free on the sea floor. It is also possible that in the Silurian some species of the atrypoid *Glassia* lived in a similar manner to that of *Aegiria*.

As for the synecology, the animal communities (Ziegler, Cocks & Bambach, 1968) in which the British species of Plectambonitacea lived during the Llandovery may be listed as follows (no plectambonitaceans have been found in the shallowest water *Lingula* Community, which is omitted):

	Eocoelia Community	*Pentamerus* Community	*Stricklandia* Community	*Clorinda* Community
Merciella vesper Lamont & Gilbert	—	—	o	—
Leangella scissa (Davidson)	—	r	c	o
Leangella segmentum (Lindström)	—	—	r	c
Eoplectodonta duplicata (J. de C Sowerby)	o	(o)	D	D
Eoplectodonta penkillensis (Reed)	—	r	o	D
Eoplectodonta duvalii (Davidson)	—	r	o	D
Ygerodiscus undulatus (Salter)	—	r	c	c
Anisopleurella gracilis (Jones)	—	—	—	D
Aegiria grayi (Davidson)	—	—	r	c

The communities listed above apply to clastic rocks deposited in level bottom basins (the brackets round the *Pentamerus* Community occurrence signifies that that community cannot be separated from the *Stricklandia* Community in the Lower Llandovery where *P. duplicata* occurs). The dashes indicate non-occurrence, r means rare, o means that it occurs sporadically, c means that it is often common in the community, and D indicates that the species may sometimes be the most dominant form found in some developments of the community. Many plectambonitids occur in limestones, particularly of Wenlock age, and animal communities have not yet been defined in these ; one of the drawbacks being the possibility of an abundance of microenvironments amongst the patch reefs and other sea-floor carbonate facies. Complete information is not yet available on the community structure of the European Silurian or of the Wenlock and Ludlow in Britain. However it is probable that the associations found in the Lower Visby Marl of Gotland and the Wenlock Shale of the Welsh Borderland may be termed *Clorinda* Communities in the same sense as that used by Ziegler *et al.*, although all the constituents are not exactly the same.

The study of the synecology of *Eoplectodonta* is particularly interesting since it apparently underwent a radical change near the beginning of Silurian time. During the Ordovician, sowerbyellids seem to have been fairly shallow water forms (Bretsky 1969), perhaps in the ecological equivalent of the *Eocoelia* Community (Bretsky 1969a). The lower Llandovery equivalent of the *Eocoelia* Community is the *Cryptothyrella* Community, and in the lower Llandovery only, the Rhuddanian, *Eoplectodonta* is found in the *Cryptothyrella* Community, for example at Mulloch Hill, Girvan, Scotland. This is the type locality of *Eoplectodonta mullochensis* (Reed), considered in this paper to be a junior synonym of *E. duplicata* (J. de C. Sowerby). That the *Cryptothyrella* Community was genuinely shallow-water is supported by the common occurrence in it at Mulloch Hill of the dasycladacean alga *Mastopora fava* (Salter), which Dr. G. F. Elliott states would only be likely to grow in a water depth of from a few centimetres to a few metres. The age of this occurrence is pre-*cyphus*

Zone (from as yet unpublished work by the present author and Dr. P. Toghill). But at approximately the same time, only a few miles away at Woodland Point, Girvan, the same species was present in a *Stricklandia* Community, and by the end of Rhuddanian time *Eoplectodonta* is found in the *Clorinda* Community, sometimes even in dominating numbers, and not at all in the shallower-water communities. Throughout the rest of the Llandovery, at least in clastic rocks, *Eoplectodonta* is one of the most characteristic members of the deeper-water *Clorinda* Community, being quite uncommon in the neighbouring *Stricklandia* Community.

The ecological niche left by the migration of the sowerbyellids from the shallower communities seems at first to have been partly filled by pholidostrophiids, and then, towards the end of Silurian time, by a great increase in the abundance of chonetids, which are rare in the Llandovery.

VI. SYSTEMATIC PALAEONTOLOGY

Superfamily **PLECTAMBONITACEA** Jones 1928

Classification.

In the Treatise on Invertebrate Paleontology, Williams (1965) classified the Plectambonitacea as follows (only families and Silurian subfamilies mentioned here):

Family Plectambonitidae Jones 1928 (Lower to Middle Ord.)
Family Taffiidae Ulrich & Cooper 1936 (Lower Ord.)
Family Leptestiidae Öpik 1933 (Lower to Upper Ord.)
Family Leptellinidae Ulrich & Cooper 1936
  Subfamily Leptellininae Ulrich & Cooper 1936 (Lower Ord. to Lower Sil.)
  Subfamily Leptellinae Williams 1965 (Lower Ord.)
  Subfamily Leptestiinae Havlíček 1961 (Middle Ord. to Upper Sil.)
Family Sowerbyellidae Öpik 1930
  Subfamily Sowerbyellinae Öpik 1930 (Ord. to Middle Dev.)
  Subfamily Ptychoglyptinae Cooper 1956 (Ord.)
  Subfamily Xenambonitinae Cooper 1956 (Middle to Upper Ord.)
  Subfamily Aegiromeninae Havlíček 1961 (Middle Ord. to Lower Sil.)
Family Bimuriidae Cooper 1956 (Middle Ord.)

Havlíček's classification (1967) of the superfamily is similar except in the following respects :

(i) Following Rõõmusoks (1963) he uses the monotypic family Anoptambonitidae (Williams put *Anoptambonites* into the Leptellininae).

(ii) He creates the new family Dubioleptinidae, to include only one species, *Dubioleptina expulsa* (Barrande), of Wenlock age, which is distinctive in the " absence of brachiophores ".

I have only briefly seen material of *Dubioleptina expulsa*, but from Havlíček's excellent illustrations, I would class the genus with the Sowerbyellinae. The loss of the " brachiophores ", which I would term here clavicular plates, is only to be expected in advanced forms after the loss of the corresponding teeth in the pedicle valve.

Thus, apart from the Dubioleptinidae, the classifications of both Williams and

Havlíček are the same for Silurian forms, and nothing in the present work suggests that substantial modifications are required.

Family **LEPTELLINIDAE** Ulrich & Cooper 1936

As stated above, the Leptellinidae can be divided into three subfamilies, the Leptellininae, the Leptellinae and the Leptestiininae, of which the Leptellinae is confined to the Lower Ordovician. Representatives of both the other subfamilies linger on into the Silurian, but, apart from *Leangella*, they are very rare.

Subfamily **LEPTELLININAE** Ulrich & Cooper 1936

Merciella Lamont and Gilbert 1945

1945 *Leptella* (*Merciella*) Lamont & Gilbert : 655.
1965 *Merciella* Lamont & Gilbert ; Williams : H376.

Lamont and Gilbert originally erected *Merciella* as a subgenus of *Leptella* Hall and Clarke, but Williams elevated it to generic rank, since the two are at least as different as the other genera in the family. The genus contains only the type species.

Merciella vesper Lamont and Gilbert 1945

(Plate 1, figs. 1–5)

1945 *Leptella* (*Merciella*) *vesper* Lamont & Gilbert : 655, pl. 4, figs. 7–12.
1965 *Merciella vesper* Lamont & Gilbert; Williams H376.

Lectotype. (Here selected) BU 369, a brachial internal mould, the original of Lamont & Gilbert 1945, pl. 4, figs. 10, 12, figured here Plate 1, figures 1 and 2.

Discussion. There is a full description of the species by Lamont and Gilbert, and this will not be repeated here. The opportunity has been taken, however, to select a lectotype, and to refigure some of the original specimens for comparison. The species is rare, and, so far as is known, confined to the Wych Beds near the Malvern Hills (Ziegler, Cocks & McKerrow 1968 : 750–7). It occurs there at several localities.

leptellininid gen. et sp. indet

(Plate 1, figs. 6–8)

Discussion. When dissolving shells from strophomenide valves in the Gray Collection, two unique valve interiors appeared, one pedicle and the other brachial, from the Woodland Formation, Lower Llandovery (Rhuddanian) of Woodland Point, south of Girvan, Ayrshire. The two specimens (now registered BB 31831–2) were not in the same box, and may not have come from identical horizons ; however the brachiopod-bearing part of the Woodland Formation is quite thin and was probably deposited quickly, and so the two valves must be of an essentially similar age.

Both specimens probably belong to the same species, as there are unlikely to be two different unknown genera of the same subfamily present at the same locality ; although the possibility must be kept in mind that they might be unrelated. They may be ascribed with some confidence to the subfamily Leptellininae on account of their general interior arrangement, which includes a distinct platform and a dorsal median septum. They are not closely related to *Merciella* (see same plate for comparison), as they differ not only in their general interior proportions, but also in the relative flatness of both valves. In addition the small size of the platform precludes reference to any known genus or species. The specimens look as if they warrant new generic and specific taxa ; however the erection of these on the scanty material available would not be desirable.

Dimensions (in mm)

	l.	w.
BB31831, pedicle internal mould	9·2	13·4
BB31832, brachial internal mould	approx. 9	13·4 (estimated)

Subfamily **LEPTESTIININAE** Havlíček 1961

There are eight nominal genera and subgenera in the subfamily Leptestiinae, *Leptestiina* Havlíček 1952 (M.–U. Ord.), *Bilobia* Cooper 1956 (M. Ord.–U. Ord.), *Diambonia* Cooper & Kindle (M.–U. Ord.), *Leangella* Öpik 1933 (M. Ord.–U. Sil.), *Leangella* (*Opikella*) Amsden 1968 (Wenlock), *Sampo* Öpik 1933 (U. Ord.), *Tufoleptina* Havlíček 1961 (Wenlock), and *Mezounia* Havlíček 1967 (Wenlock). As may be seen, four of these occur in the Silurian, whilst the other four appear to be confined to the Ordovician. In this study *Tufoleptina* is considered a synonym of *Leangella* and *Opikella* retains the subgeneric rank which Amsden proposed for it. The genus *Mezounia* (Havlíček 1967 : 31, pl. 2, figs. 7–10, 13–15) is represented only by its type species, *M. bicuspis* (Barrande 1879), from several localities in the Bohemian Liteň Shales (Wenlock). It is a small form, 6·5–8·5 mm wide, but shows a clearly-developed platform and subperipheral rim. As yet no material attributable to the genus is known, apart from that used in the original description, and its phylogenetic position is enigmatic.

Havlíček (1967 : 29) also places *Tetraodontella* Jaanusson (1962 : 1) within the Leptestiininae, but its brachial valve interior is unlike the rest of the group, and I follow Williams (1965 : H376) in placing it with *Isophragma* Cooper 1956.

Leangella Öpik 1933

1928 *Leptelloidea* Jones *pars* (*non Leptelloidea* s.s.) : 385.
1933 *Leangella* Öpik : 42.
1953 *Leangella* Öpik : 14.
1961 *Tufoleptina* Havlíček : 447.
1965 *Leangella* Öpik ; Williams : H378.
1965 *Tufoleptina* Havlíček ; Willliams : H378
1967 *Tufoleptina* Havlíček : 33.
1968 *Leangella* (*Opikella*) Amsden : 48.

TYPE SPECIES (by original designation) : *Plectambonites scissa* (Salter) var. *triangularis* Holtedahl 1916, the subspecies elevated to species rank as *Leangella triangularis* (Holtedahl) by Öpik (1933 : 42).

DISCUSSION. As well as the type, Öpik put four species into his new genus, *L. scissa* (Salter), *L. segmentum* (Lindström), *L. sholeshookensis* (Jones) and *L. septata* (Cooper). Since that time Cooper & Kindle (1936 : 356) erected the genus *Diambonia* for species similar to *Leangella*, but with a median septum in the pedicle valve, which would include *septata*. The type specimens (GSM 37538, GSM Pg162, GSM Pg225, and GSM Pr107) of *L. sholeshookensis* from the Upper Ordovician Slade Beds of Carmarthenshire have been re-examined ; the species is not a *Leangella* or *Diambonia*, and may even lie outside the subfamily. Another species, *discuneata*, originally described as a *Leangella* (Lamont 1935 : 315), from the Lower Drummuck Group (Ashgill) of Girvan, Ayrshire, possesses a median septum in the pedicle valve, and is here transferred to *Diambonia*. The type specimens are re-illustrated here (Plate 1, figs. 9, 10). True *Leangella* does, however, exist in the Ordovician, for example *Leangella hamari* Spjeldnaes (1957 : 81, pl. 2, figs. 1–3). As far as is known, *Diambonia* became extinct before the close of the Ordovician, as did *Sampo*, which has a denticulate hinge line.

In 1961 Havlíček erected the genus *Tufoleptina*, with type and only species *T. tufogena* Havlíček from the ashy Wenlock Upper Liteň Shales in Bohemia. Havlíček (1967 : 33) states that the genus is extremely close to *Leangella*, but differs " because a conspicuous submarginal ridge is developed in its pedicle valve, which in *Leangella* is absent. " In fact, however, this ridge is variably developed in *Leangella* (e.g. Plate 2, fig. 2), and even occurs in topotype specimens of *Leangella triangularis* itself (Öpik 1933, pl. 8, fig. 6 shows the ridge clearly). Thus the two genera are placed in synonymy. Dr. Havlíček kindly led me to the type locality of *Leangella tufogena*, where a good sample was obtained (Plate 4, figs. 5, 6) which clearly demonstrates its close relationship with the contemporary *Leangella segmentum*, but differences in proportion and shape of the subperipheral rim are enough to keep the two species separate.

Amsden (1968 : 48) has erected a subgenus of *Leangella*, named *Opikella*, with, as type and only species, *L.* (*O.*) *dissiticostella* Amden from the Wenlock St Clair and Clarita Limestones of Arkansas and Oklahoma. It is said to differ from *Leangella* s.s. in having no secondary parvicostellae between the primary costellae. No other species of *Leangella* examined by the present writer lacks these secondary costellae, although in many individuals they cannot be seen owing to indifferent preservation. Thus it seems best to endorse Amsden's choice of subgeneric rank for *L.*(*O.*) *dissiticostella*, illustrating the close relationship between *Opikella* and *Leangella* s.s.

Although Foerste (1903 : 708) did not illustrate his *Plectambonites tennessensis* from the Waldron Shale, near Clifton, Tennessee, Dr. G. A. Cooper has kindly sent over a batch of specimens (BB 31843–54) on exchange labelled *Leangella tennessensis*. They are from a quarry in the Waldron Shale, on Tennessee Route 13, 1·1 miles north of the junction with U.S. highway 64, north of Waynesboro, Tennessee. The species may be definitely attributed to *Leangella* s.s (it certainly has secondary parvicostellae

and seems very close to *Leangella tufogena*, rather than *L. segmentum*, both of which are contemporary.

Species assigned to Leangella

L. triangularis (Holtedahl 1916)
L. (*Opikella*) *dissiticostella* Amsden 1968
L. hamari Spjeldnaes 1957
L. ino Öpik 1953
L. scissa [Salter MS] (Davidson 1871) = *L. woodlandensis* (Reed 1917)
L. segmentum [Angelin MS] (Lindström 1861)
L. tennessensis (Foerste 1903)
L. tufogena (Havlíček 1961)

Leangella triangularis (Holtedahl)

1916 *Plectambonites scissa* (Salter) *triangularis* Holtedahl : 84–5, pl. 15, figs. 5–6.
1933 *Leangella triangularis* (Holtedahl) Öpik : 42–48, pl. 8, figs. 6–8, pl. 9, figs. 1–4.

Discussion. Öpik has already described *Leangella triangularis* so well that a further detailed description will not be given here. There are however one or two small points to make. Öpik describes and illustrates (1933 text-fig. 7 and pl. 9, fig. 2) calcareous outgrowths on the exterior of both valves, which he terms (1933 : 46) comae. I have looked without success in British species for this structure, although admittedly most contemporary material is from clastic rock, rather than the limestones typical of the Baltic region. Öpik describes the comae as having a mass many times larger than the shell which carries it, and as being a rock-forming factor. I have shown Öpik's illustrations to Dr. G. F. Elliott, who considers that these comae may very well be adherent calcareous algae, rather than true outgrowths of the brachiopod exoskeleton. However, true comae are apparently recorded in the Plectambonitacea, and are illustrated schemetically for *Bimuria* by Williams (1965 : H78), but there is no evidence that they ever reached the large proportions suggested by Öpik for *Leangella*.

As already noted in the discussion of the genus, *Leangella triangularis* possesses a subperipheral rim near the pedicle valve margin (Öpik 1933, pl. 8, fig. 6), admittedly variably developed, which was the feature which Havlíček thought it lacked when he erected *Tufoleptina*. It is quite clear from Öpik's section (1933, pl. 9, fig. 2) that the purpose of this subperipheral rim was to fit snugly into the corresponding structure in the brachial valve, forming a tight fit when the two valves were closed.

Leangella scissa [Salter MS] (Davidson)

(Plate 1, figs. 11–14, Plate 2, figs. 1–14, Plate 3, figs. 2–11, Plate 4, figs. 1–4)

1866 *Leptaena scissa* Salter MS *in* Ramsay : 267 (*nomen nudum*).
1867 *Leptaena scissa* Salter MS *in* Murchison : 210, 525 (*nomen nudum*).
1871 *Leptaena scissa* [Salter MS] Davidson : 325, pl. 47, figs. 21–23, *non* figs. 24, 25.
1883 *Leptaena scissa* Salter ; Davidson : 170, pl. 12, fig. 22.
non 1916 *Plectambonites scissa* (Salter) var. *triangularis* Holtedahl. : 84, pl. 15, figs. 5, 6.

1917 *Plectambonites scissa* (Salter) Reed : 880, pl. 14, figs. 34, 35.
1917 *Plectambonites segmentum* (Angelin) var. *woodlandensis* Reed : 881, pl. 14, figs. 36–41.
1928 *Leptelloidea scissa* (Davidson) Jones : 481, pl. 25, figs. 8–12.
1933 *Leangella scissa* (Salter) Öpik : 42.
1965 *Leangella scissa* (Salter) ; Williams : H378, fig. 242, 2a–c.

Diagnosis. *Leangella* with relatively few primary costae, diamond-shaped halves of the brachial valve platform and a pyriform subperipheral rim in the brachial valve, variably developed in the pedicle valve.

Description. *Exterior.* Pedicle valve very convex, almost semicircular in lateral profile ; brachial valve concave, though flatter than the pedicle valve. Umbo inconspicuous but the pedicle valve may be slightly enrolled over the hinge line. Valve outline is semicircular to sub-triangular, maximum width at hinge line or slightly anterior of it. Size of apparent adults varies from population to population, from a maximum of less than 4 mm wide (B_3beds (Idwian) of Llandovery) up to 13 mm wide (Newlands Sandstone (Idwian) of Girvan). Ornament parvicostellate, with between 4 and 14 primary costae, with extremely fine costellae between them, invisible in poor specimens. Spacing between primary costae regular ; near the margin other larger ribs sometimes arise by intercalation. Growth lines not usually seen, except near the margins of large valves. Small rugae sometimes developed near the ears, particularly on pedicle valve, but they do not meet medianly or occur over the whole shell. Interareas relatively large, occasionally with strong growth lines parallel to the hinge line, oriented more or less in the same plane as the valve margins and each other. Central structures are as illustrated by Öpik (1933, text-fig. 7a) for *L. triangularis*, apart from the deltidial plate being laterally thinner, and more triangular at the valve apex, rather than having a pointed arch. Brachial valve structures identical, consisting of a prominent central shaft, with edges of lateral processes showing from the exterior, sometimes bifurcating to accommodate the diductor muscle. There are a pair of small discrete chilidial plates. Apical foramen occasionally seen in very well-preserved small specimens, usually slightly off centre.

Pedicle Valve Interior. Hinge line smooth. Strong teeth are widely divergent. Anteriorly they are part of the same structure as weak dental plates, which continue into muscle bounding ridges, which in turn are elevated medianly to form a positive muscle platform. No median septum. Muscle platform mainly of adventitious shell material, and in gerontic specimens two types of markings occur on platform floor, concentric growth lines (up to 20 sometimes visible) and striae (normally only two or three on each half of the platform) running approximately antero-posteriorly, representing the minor subdivisions of the muscles. Growth lines continuous between two halves of platform, over the small median swell, too slight to be termed a ridge. Although differentiation between adductor and diductor fields is not seen in most specimens, it may be observed in some (Plate 2, figs. 9, 13), in which the diductors are small and narrow, sometimes not even extending to the anterior margin of muscle platform, in contrast with the large bulk of the adductor muscles, which occupy most of the platform area. Vascular markings (e.g. Plate 2, figs. 2, 9, 12 and 14) consist of two large trunks commencing from underneath the anterolateral portions of muscle platform, converging slightly centrally, coming a long way

anteriorly and swinging apart at an acute angle, continuing sub-parallel with anterior valve margin, just posterior of the subperipheral rim (when present). They continue right round until they nearly return to the hinge line, usually fading out just laterally of the muscle platform again. From these main trunks small branches come off at right angles anteriorly. Subperipheral rim variably developed ; it can be seen laterally in most specimens, cutting off the cardinal angles, but only rarely extending anteriorly. Size of papillae small for genus.

Brachial Valve Interior. Hinge line smooth. Cardinal process usually trifid with prominent shaft, but occasionally the lateral processes are themselves split. Socket plates prominent, massive and widely divergent, curving round to become sub-parallel with hinge line (Plate 2, fig. 4), although sometimes the socket plates are shorter and stubbier, but projecting further into the pedicle valve (e.g. Plate 3, fig. 4). Socket plates connected by low lateral ridge to platform, which becomes more elevated anteriorly. Antero-lateral margins of platform are straight, apart from slight frilling ; anteriorly changing direction sharply by a right angle or more, before uniting to form a w shape for the whole field (Plate 2, fig. 4). No median septum, but on the platform floor there is a slight swell dividing the attachment area of the adductors. On most specimens radial striae are present on platform floor (Text-fig. 1). The flaring forward of the platform from the valve floor, together with the anterior fold of the platform in the direction of the pedicle valve, combines to form a conical hole under the antero-median part of the platform (seen as a mould in Plate 2, fig. 7), the " Tubus " of Öpik (1933, pl. 9, fig. 4, text-fig. 17). Vascular markings not so impressed as in the pedicle valve, although faint traces run antero-posteriorly (similar to Öpik 1933, pl. 8, fig. 7). Subperipheral rim well developed in all specimens, more pronounced than in pedicle valve : outline pyriform, with marked anterior constriction and gentle slope on its interior, but on side facing valve margins the angle is more abrupt, with the ridge usually nearly perpendicular, sometimes even overhanging.

Type Specimens. Davidson (1871, pl. 47, figs. 21–25) figured five specimens as *Leptaena scissa* ; fig. 21 from the Upper Llandovery of Norbury, Shropshire, England, figs. 22 and 23 from the Lower Llandovery Gasworks Mudstone, Pembrokeshire, Wales and figs. 24 and 25 from the " Caradoc ; Sholes Hook ", also of Pembrokeshire. Thus the originals of all these figures are available as syntypes. However, Jones (1928 : 48 *et seq.*) discussed the nomenclatorial and identification problems, and removed the Ordovician specimens (Davidson's figs. 24 and 25) to *Sowerbyella quinquecostata.* He also talked of "the type locality at the Gasworks, Haverford-west ", but failed to designate any type specimen. Since that time the Gasworks has been taken as the type locality for *L. scissa,* and so I here formally select the original of Davidson 1871, pl. 47, fig. 23 as lectotype. Davidson's original is also the same pedicle valve internal mould (GSM 11364) which was figured by Jones (1928, pl. 25, fig. 8). The originals of Davidson's figs. 21 and 22 seem to be lost, although the original of Davidson 1883, pl. 12, fig. 22, from Hope Quarry, Shropshire, is in the Davidson Collection (B 13673, Plate 2, fig. 13).

Localities and material. Gasworks Mudstone (Lower Llandovery, Rhuddanian), lane opposite entrance to the Gasworks, Haverfordwest, Pembrokeshire, Wales.

Grid Ref. SM/9588 1533 (GSM 11364 etc., BB 31824–9, BB 32136–67 etc.) Plate 1, figs. 11–14, Plate 2, figs. 1–4).

A_4 beds (lower Llandovery, Rhuddanian), Cwm Rhyddan quarry, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7623 3250. (BB 32107 etc.)

Woodland Formation (Lower Llandovery, Rhuddanian), Woodland Point, south of Girvan, Ayrshire, Scotland. Grid Ref. NX/168 952 (B 44618–23, BB 31836, BB 31975–80 etc.) (Plate 2, figs. 5–7).

Newlands Sandstone (Middle Llandovery, early Idwian), Newlands Farm, Craighead Inlier, near Girvan, Ayrshire, Scotland. Grid Ref. NS/2777 0432. (B 73641–4 etc.) (Plate 3, figs. 2–4).

Horizon V_2c (Rhuddanian or Idwian), east bank of River Banwy, west of Upper Hall Farm, near Meiford, Montgomeryshire, Wales. Grid Ref. SJ/1326 1058. (BB 31929–48).

B_3 beds (Idwian), old quarry, south side of Cilgwyn-Myddfai road, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7605 3093 (BB 32085–94).

Venusbank Formation (late Idwian and early Fronian), Hope Quarry, south of Minsterley, Shropshire, England. Grid Ref. SJ/3551 0208. (B 13673 etc. OUM C9121–39) (Plate 2, figs. 8–14).

Temporary exposure in field near Wilmington, Shropshire. Grid Ref. SJ/3061 0246. (GSM 85282–8) (Plate 3, figs. 5–10).

C_1 beds (Fronian), Sefin Shales, near old footbridge, south of Letty'r-hyddod, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7418 2812. (BB 32095–106) (Plate 4, figs. 1–4).

C_4 beds (Telychian), quarry on Cefn-Cerig road, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7741 3235. (BB 31675–6 etc.) (Plate 3, fig. 11).

Dimensions (in mm)

	l.	w.
BB 31824 pedicle internal mould, Gasworks (Plate 1, fig. 11)	5·9	8·3
BB 31825 pedicle internal mould, Gasworks (Plate 2, fig. 2)	6·2	8·3
BB 32158 brachial external mould, Gasworks	3·2	6·0
B 73641 brachial internal mould, Newlands (Plate 3, fig. 4)	approx 8	approx. 13
BB 31855 brachial internal mould, Newlands	2·4	4·8
OUM C9136 pedicle internal mould, Hope Quarry (Plate 2, fig. 14)	8·3	8·9

Discussion. *Leangella scissa* probably evolved into *Leangella segmentum* gradually during the upper part of the Llandovery (Telychian). By preceding Fronian times, populations occur such as that at Wilmington, Shropshire (Plate 3, figs. 5–10) which although referable to *L. scissa*, yet contain occasional individuals (Plate 3, figs. 9, 10) which possess circular ω, as opposed to w shaped platforms, although the pyriform shape of the subperipheral rim in the same individual is typical of *L. scissa*. By early Telychian times, however, populations may be found with the characteristic

semi-circular subperipheral rim of *L. segmentum*, although the form of the platform of the figured specimen (Plate 3, fig. 11) is still close to *L. scissa*. How foreign species such as *L. triangularis*, *L. tufogena* and *L. tennessensis* fit into this pattern is not certain ; only one population of each has been available for this study. These three species have not yet been reported from outside their topotypic formations, so that further work could reveal them as varietal populations of the *scissa-segmentum* stock. Fortunately for nomenclature, *scissa* and *segmentum* are the two senior species names in *Leangella*.

The occurrence of *Leangella* is variable, in many apparently favourable localities it is quite absent, at other times it occurs rarely (in many other localities than detailed above), and occasionally in abundance, such as in some horizons of the Hughley Shale of the Church Stretton boreholes (Cocks & Rickards 1969).

Leangella segmentum [Angelin MS] (Lindström)

(Plate 3, fig. 1, Plate 4, figs. 7–12)

1861 *Leptaena segmentum* Angelin Lindström : 374.
1871 *Leptaena segmentum* Angelin ; Davidson : 321, pl. 48, figs. 28–30.
non 1883 *Leptaena segmentum* Angelin var. *cornuta* Davidson : 166, pl. 12, figs. 1–3.
non 1917 *Plectambonites segmentum* (Angelin) var. *woodlandensis* Reed : 881, pl. 14, figs. 36–41.
1928 *Leptelloidea segmentum* (Lindström) Jones : 485, pl. 25, figs. 13–18.
1933 *Leangella segmentum* (Lindström) Öpik : 42, text-fig. 8.
1965 *Leangella segmentum* (Lindström) ; Williams : H378, fig. 242, 2d.

Diagnosis. *Leangella* with as many as 20 primary costae, ω shaped brachial valve platform and approximately semicircular subperipheral rim in the brachial valve, variably developed in the pedicle valve.

Description. *Exterior*. Pedicle valve convex, though normally less than *L. scissa* ; brachial valve concave. Umbo variably developed, often inconspicuous. Enrollment of pedicle valve over hinge line less than *L. scissa*. Valve outline semicircular, maximum width at hinge line, or just anterior to it. Size range comparable with *L. scissa*, with width only rarely exceeding 10 mm. Ornament parvicostellate, with between 8 and 20 primary ribs with fine costellae between them. Although most of the larger ribs originate at the umbo, some also arise by intercalation anteriorly, more than in *L. scissa*, apparently causing the difference in numbers of larger ribs. Growth lines usually inconspicuous, except near anterior margin, but may rarely be seen over most of valve (Plate 4, fig. 7). Occasionally very prominent growth lines occur, anterior of which costae may be laterally displaced (also seen on Plate 4, fig. 7), presumably as a result of damage or modification of individual setae during mantle regression (perhaps due to adverse conditions or a breeding pause) and different positioning when mantle transgression resumed. Small rugae occasionally developed, confined to lateral extremities. Interareas relatively large, orientation similar to that found in *L. scissa* (Plate 4, fig. 8), apart from the small pair of deltidial plates, which appear to be closer in shape to those in *L. triangularis*. Apical foramen preserved more often than in *L. scissa* ; protegular node often seen in the pedicle valve.

Pedicle Valve Interior. In the type collection from Djupvik there are only three pedicle interiors, of indifferent preservation, but good enough to substantiate the following, chiefly based upon English material from the Wenlock Limestone and Buildwas Beds.

Hinge line smooth. Teeth strong and divergent, continuing weakly anteriorly as dental plates, themselves continuing round as the muscle platform. Outline of platform bilobed. No median septum. Muscle platform floor has same structures, growth lines and radial striae as *L. scissa*. Muscle scars also similar to *scissa*, with most of platform area occupied by adductor scars. Vascular markings occasionally seen as a pair of double mantle canals running anteromedianly from beneath anterior edges of muscle platform lobes rarely seen to swing round parallel to the valve margin. Subperipheral rim parallel with valve margin, often well impressed, particularly in Wenlock Shale material. The taleolae sometimes prominent, particularly in the region just posterior of the subperipheral rim.

Brachial Valve Interior. Hinge line smooth. Cardinal process trifid posteriorly (Plate 4, fig. 8), but anteriorly bifurcating and recombining, to forming slight depression and then central swell in the platform. No median septum. Strong socket plates connected anteriorly with platform. Considerable variation in shape, proportions, relative size and antero-median fold strength of the platform even within a population (Plate 4, figs. 9–12). Strong subradial striae often on the platform. Vascular markings occur parallel ridges running antero-posteriorly from anterior edge of the platform, occasionally to the edge of the subperipheral rim. On the trail there are variable grooves corresponding with the external main costae (Plate 4, figs. 10, 11). Subperipheral rim strong, usually uniformly semi-circular, but rarely with the anterior pyriform stricture so strongly developed in *L. scissa*. Coarse papillae outside platform and inside subperipheral rim, but fine papilla on the trail.

Type specimens. Lectotype (here chosen) Naturhistoriska Riksmuseet, Stockholm, RMS Br 31598, a brachial valve showing the interior (Plate 4, fig. 11) from the Mulde Marl (Upper Wenlock) of Djupvik, Gotland, Sweden. The specimen was collected and labelled by Angelin as "*Leptaena segmentum* Ang." and curated by Lindström (RMS Br 31598–701), thus available to the latter as syntype material in 1861.

Dimensions (in mm.)

	l.	w.	h.
All the specimens are from Djupvik.			
RMS Br 31598 brachial valve, lectotype (Plate 4, fig. 11)	5·3	8·2	—
RMS Br 31602 conjoined valves (Plate 4, figs. 7, 8)	5·2	8·5	1·9
RMS Br 31603 ,, ,,	5·7	10·0	2·3
RMS Br 31604 ,, ,,	5·9	8·7	2·3
RMS Br 31605 ,, ,,	5·6	9·6	2·3
RMS Br 31606 ,, ,,	3·5	6·9	1·1

Discussion. *Leangella segmentum* is a widely quoted species from many stratigraphical levels within the Silurian. The name is really due to Angelin, who gave away and sold many specimens labelled *segmentum* in sets of fossils from Gotland from the 1830's onwards, but it was not until 1861 that the name was properly published (by Lindström), and even then without illustration. The present illustrations (Plate 4, figs. 7–12) are the first of Gotland material, despite the appearance of the name in many faunal lists (e.g. Hede 1960). The opportunity has also been taken to select a lectotype.

The vertical range of the species is not entirely certain. As discussed above, *L. segmentum* probably evolved from *L. scissa* during the late Landovery, and the form occurring in the Telychian Hughley Shales of Shropshire is closer to *segmentum* than to *scissa*. During the Wenlock, *Leangella segmentum* flourished in local swarms, particularly in muddy environments, such as the Lower Wenlock Buildwas Beds of Shropshire and in parts of the Upper Wenlock Mulde Marl of Gotland. The species also occurs rarely in limestones (Plate 3, fig. 1). British Wenlock forms and their distribution will be dealt with by Dr. M. G. Bassett in the course of his forthcoming monograph. He has discovered a population in the Wenlock Shale of the Usk Inlier, Monmouthshire, Wales, with consistently different internal and external proportions, which may merit subspecific status. *Leangella* is rare in the Ludlow, but is known from at least the lower part of the Series in Wales and the Welsh Borderland. There are no British records from higher horizons than the Eltonian (Shergold & Shirley, 1968).

Family **SOWERBYELLIDAE** Öpik 1930

Williams (1965) includes four subfamiles within this family, the Sowerbyellinae Öpik 1930, the Ptychoglyptinae Cooper 1956, the Aegiromeninae Havlíček 1961 and the Xenambonitinae Cooper 1956. All four were flourishing by Middle Ordovician time, but only the Sowerbyellinae and the Aegiromeninae survived to the Lower Silurian. Since these two subfamilies diverged so long before the period of the present study, they will be considered quite separately here.

Subfamily **SOWERBYELLINAE** Öpik 1930

There are at the moment twelve nominal genera or subgenera within this subfamily, as follows:—

Sowerbyella Jones 1928, type species *S. sericea* (J. de C. Sowerby)
Viruella Rõõmusoks 1959, type species *V. liliifera* (Öpik)
Anisopleurella Cooper 1956, type species *A. tricostellata* Cooper
Eochonetes Reed 1917, type species *E. advena* Reed
Eoplectodonta Kozlowski 1929, type species *E. precursor* (Jones)
Thaerodonta Wang 1949, type species *T. aspera* Wang
Ygera Havlíček 1961, type species *Y. ygerens* Havlíček, a junior synonym of *Y. sowerbyana* (Barrande)

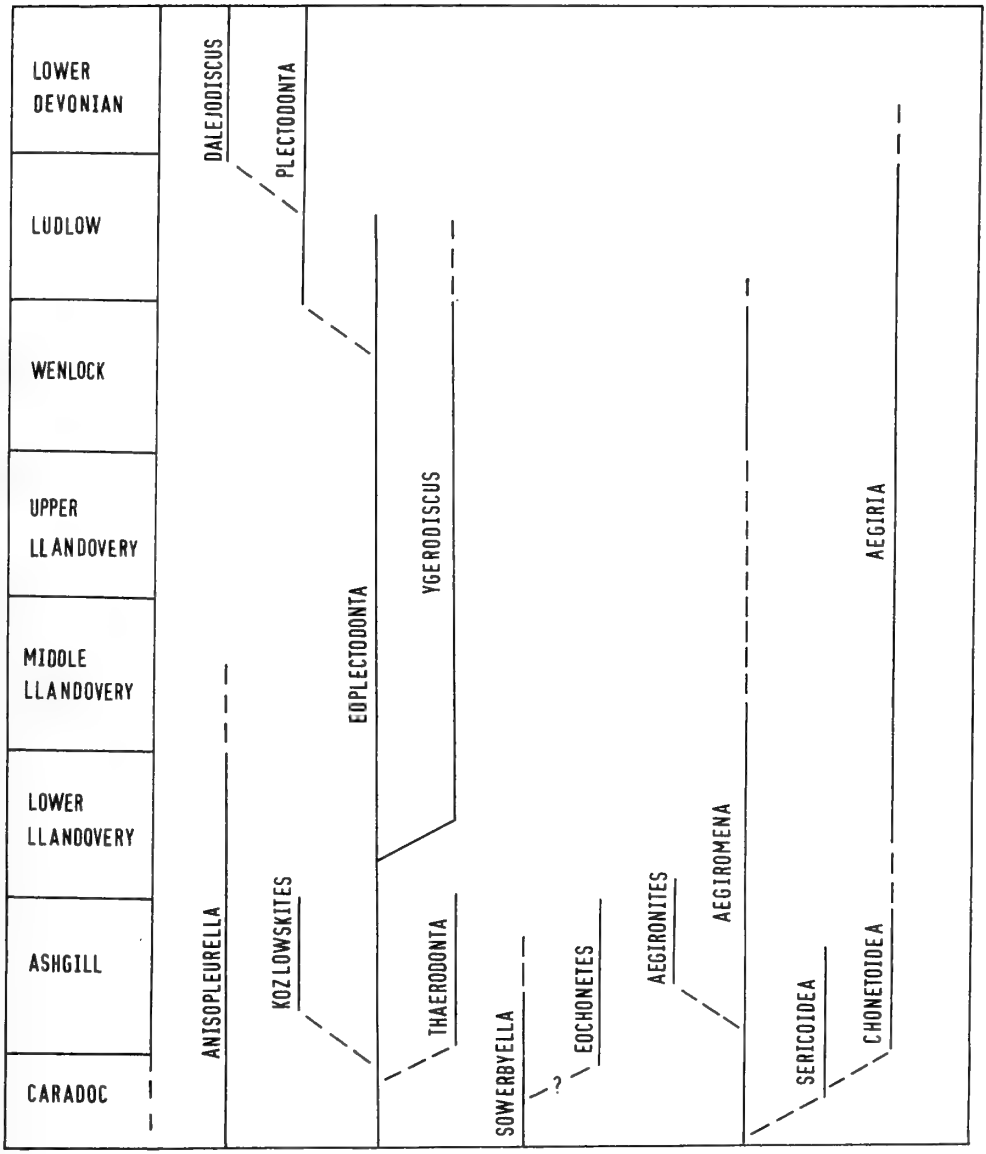

FIG. 6. Possible phylogeny of the Sowerbyellidae from the Upper Ordovician to the Lower Devonian.

Ygerodiscus Havlíček 1967, type species *Y. undulatus* (Salter)
Plectodonta Kozlowski 1929, type species *P. mariae* Kozlowski
Dalejodiscus Havlíček 1961, type species *D. comitans* (Barrande)
Plectodontella Havlíček 1953, type species *P. redunca* Havlíček
Kozlowskites Havlíček 1952, type species *K. nuntius* (Barrande)

Of these genera, only three, *Sowerbyella*, *Viruella* and *Anisopleurella*, do not bear denticles on the hinge line, and all these have their type species from near the base of the Caradoc. A fourth genus *Eochonetes*, whilst not denticulate, has a most distinctive perforated hinge line. In the examination of a large number of populations of Sowerbyellinae, no population has been seen from the Silurian which does not possess a denticulate hinge line. Thus, contrary to previous records, it seems likely that *Sowerbyella* became extinct before the close of the Ordovician and that all Llandovery and later Sowerbyellinae may be referred to *Eoplectodonta* and its later derivatives, namely *Ygerodiscus*, *Plectodonta*, *Plectodontella* and *Dalejodiscus*. The last two genera have only been recorded from the post-Ludlovian of Europe, and it is also possible that *Plectodonta* may be post-Ludlovian, although the Upper Silurian faunas have not yet been closely studied, apart from in Bohemia. The only exception is *Anisopleurella*, a chiefly Ordovician genus with a smooth hinge line, which lingered on to occur rarely in the Silurian.

There can be no doubt that some sowerbyellids have highly developed plicae, whilst others do not. This was recognized in Jones's division (1928 : 397) of *Sowerbyella* into various groups, chiefly based on the external form of the shell. The plicate group Jones termed the '*undulata*-group' and this seems essentially the basis upon which Havlíček (1967) erected his new genus *Ygerodiscus*, with *undulata* as type species. This genus is accepted as valid in the present paper. However, there is always some variability in shell undulation, as there is also in rugation. In every population examined there are some individuals showing rugae in the posterior region, sometimes confined to the ears, sometimes spread some way along the hinge line, and in occasional individuals an odd ruga may go right across the whole shell. This rugation cuts across the radial ornament, in contrast with one of Jones's other groups, the 'subcorrugatella group' in which the small rugae are interrupted by the costellae, a form of ornament seen elsewhere in the Plectambonitacea, for example in *Pytchoglyptus*, and which homoeomorphically arises in other groups of the Strophomenida, for example in the strophomenaceans *Pentlandina* and *Cyphomena* (*Cyphomenoidea*) (Cocks 1968).

Eoplectodonta Kozlowski 1929

1929 *Plectodonta* (*Eoplectodonta*) Kozlowski : 112.
1956 *Eoplectodonta* Cooper : 807.
1961 *Ygera* Havlíček : 449.
1965 *Eoplectodonta* (*Eoplectodonta*) Williams : H381.
1967 *Ygera* Havlíček : 58.

Type species (by original designation) ; *Sowerbyella precursor* Jones 1928, from the Lower Llandovery of Pembrokeshire, Wales. As outlined below, this species is

considered here as a junior subjective synonym of *Leptaena duplicata* J. de C. Sowerby (*in* Murchison 1839).

Discussion. *Eoplectodonta* is treated here as a genus separate from *Plectodonta*, rather than as the subgenus originally created by Kozlowski. The differences between the two genera are as follows (the observations on *Plectodonta* are based on topotype material of *P. mariae*, B. 81370–8 (figured here Plate 16, figs. 10–12), sent to the British Museum in an exchange with the University of Warsaw in 1932).

Plectodonta	*Eoplectodonta*
Non-alate, with rounded hinge margins	Alate
Umbo not incurved, open cardinal area	Enrolled hinge line in adults
Deltidium present, with reduced chilidium	Open delthyrium, with conspicuous chilidial plates

That *Plectodonta mariae* is only developed to half the usual size of *Eoplectodonta*, and also possesses more than double the number of primary costellae, are regarded as specific, rather than generic, features. In addition *P. mariae* is much more strongly papillose in the interior than *Eoplectodonta*, more approaching the condition seen in *Aegiria*, but this too may be merely a specific character. The general arrangement of the brachial valve interiors, although differing in the relative emphasis of some structures, is, however, essentially similar in both genera, and the descent of one from the other at some time in the late Silurian seems highly probable.

In the Treatise on Invertebrate Paleontology, Williams (1965) put *Thaerodonta* Wang into synonomy with *Eoplectodonta*, and *Kozlowskites* Havlíček as a subgenus of the latter. Both these other genera are known only from the Upper Ordovician. *Kozlowskites*, known only from the Ashgill of Bohemia, differs from *Eoplectodonta* in some relatively minor details of the pedicle valve, as discussed by Havlíček (1967 :56), and Williams' subgeneric arrangement seems correct. However in the present paper *Thaerodonta* is retained as generically distinct from *Eoplectodonta* as it differs fundamentally in having denticles in the brachial valve and fossettes in the pedicle valve as opposed to the other way round in *Eoplectodonta* (Wang 1949 : 19, pl. 11).

Apart from *Ygerodiscus*, discussed below, the only other Silurian genus closely related to *Eoplectodonta*, is *Ygera* Havlíček (1961, 1967). To this genus Havlíček (1967 : 58) refers four species, *Y. sowerbyana* (Barrande), *Y. bidecorata* (Barrande), both from the Bohemian Wenlock, and *Y. lata* (Jones) and *Y. transversalis* (Wahlenberg), from the Wenlock of England and Gotland respectively. In addition Havlíček attributes " *Y.* cf *lata* (Jones 1928) ; Llandovery, U.S.S.R. (Podolia) " (Nikiforova 1954 : 76, pl. 7, figs. 1, 2). He states that " *Eoplectodonta* differs from the related genus *Ygera* in the presence of a well-developed median septum in the brachial valve and ill-defined lobes of visceral field. . . . *Thaerodonta* fairly resembles *Ygera* ; it is mainly distinguished in having small teeth on the cardinal margin of brachial valve, while in *Ygera* the case is opposite, as the denticulate cardinal margin occurs in the pedicle valve " (Havlíček 1967 : 58).

Dr. Havlíček was kind enough to lead me to the locality Hliník in Bohemia (the type locality of his earlier *Ygera ygerens*, which he subsequently put into the synonomy of *sowerybana*) where a large sample of *Ygera* was obtained (Plate 13, figs. 2,

4–6, 8, 9). Contrary to his report, denticles do occur in the pedicle as well as the brachial valve. The septal structures are variable, but within the range of variability of *Eoplectodonta*. Thus, although *sowerbyana* may be recognized as a distinct species, *Ygera* is regarded in this paper as a junior synonym of *Eoplectodonta*.

The following Silurian species are assigned to *Eoplectodonta* :—

Leptaena duplicata J. de C. Sowerby 1839 (synonyms *Plectambonites mullochensis* Reed 1917, *Plectambonites tricostata* Reed 1917, *Sowerbyella precursor* Jones 1928, *Sowerbyella superstes* Jones 1928).

Anomites transversalis Wahlenberg 1819.

Plectambonites penkillensis Reed 1917 (synonyms *Sowerbyella millinensis* Jones 1928, *Sowerbyella canastonensis* Jones 1928, *Sowerbyella parabola* Jones 1928).

Leptaena duvalii Davidson 1847 (the Wenlock " *transversalis* " of many authors ; synonym *Sowerbyella lata* Jones 1928).

Leptaena sowerbyana Barrande 1848 (synonym *Ygera ygerens* Havlíček 1061).

Strophomena bidecorata Barrande 1879.

The following species may be referable to *Eoplectodonta*, but have not yet been re-investigated :—

Sowerbyella elegans Poulsen 1943 : 16, pl. 2, fig. 4. Upper Llandovery (*sedgwickii* Zone), Offley Island, Greenland.

Plectambonites tenera Shaler 1865 : 64, no illustration (put in synonomy of *transversalis* by Twenhofel 1928 : 192). Gun River and Jupiter Formations (Middle and Upper Llandovery), Anticosti Island, Canada.

Sowerbyella minuta Kul'kov 1967 : 67, pl. 1, figs 7–9. Upper Wenlock of the Altai Highlands, U.S.S.R.

Plectodonta exceptionis Rybnikova 1967 : 189, pl. 19, figs. 8–12. Lower to Middle Landovery from boreholes in Latvia, U.S.S.R.

Of these last four species, *elegans* appears from Poulsen's illustrations to be small *Eoplectodonta*—the form of the adults remains unknown, and *tenera* requires proper definition and illustration. *P. exceptionis* is adequately illustrated, and may be a distinct species, probably related to *E. penkillensis*. *S. minuta* is poorly described and illustrated, and although it appears to be a sowerbyellid, the figures are too poor and description too general to say more.

There is also a small group of species which have been described from the Upper Silurian or Lower Devonian of central Europe :—

Leptaena minor Roemer 1854 : 12, pl. 3, fig. 1.

? *Plectambonites minor* var. *digitata* Wolburg 1933 : 53, pl. 2, fig. 6.

Plectodonta minor var. *alatiformis* Schmidt 1939 : 83, text-fig. 6.

Plectodonta thuringica Schmidt 1939 : 80, pl. 3, figs. 1–2.

It is quite possible that some of these names are synonyms of each other, but the genus to which they belong is uncertain, and the whole of this small group is in need of revision, together with the distribution of *Plectodonta* itself.

Eoplectodonta duplicata (J. de C. Sowerby)

(Plate 5, figs. 1–12, Plate 6, figs. 1–13, Plate 7, figs. 1–11, Plate 8, figs. 1–11)

1839 *Leptaena sericea* var. J. de C. Sowerby *in* Murchison : 636, pl. 19, fig. 2.
1839 *Leptaena duplicata* J. de C. Sowerby *in* Murchison : 636, pl. 22, fig. 2.
1871 *Leptaena transversalis* (Wahlenberg); Davidson *pars* : 318, *non* pl. 48, figs 1–9.
1917 *Plectambonites transversalis* (Dalman) ; Reed : 886, pl. 15, figs. 35, 36.
1917 *Plectambonites transversalis* var. *duvali* (Davidson) ; Reed : 887, pl. 15, figs. 37–40.
1917 *Plectambonites transversalis* (Dalman) var. *mullochensis* Reed : 887, pl. 15, figs. 41, 42, pl. 16, figs. 1, 2.
1917 *Plectambonites transversalis* (Dalman) var. *tricostata* Reed : 889, pl. 16, fig. 8–13.
1928 *Sowerbyella duplicata* (J. de C. Sowerby) Jones : 432, pl. 22, figs. 6–13, pl. 23, figs. 1, 2.
1928 *Sowerbyella precursor* Jones : 437, pl. 23, figs. 3–5.
1928 *Sowerbyella mullochensis* (Reed) Jones : 439, pl. 23, figs. 6–9.
1928 *Sowerbyella superstes* Jones : 441, pl. 23, figs. 10–12.
1928 *Sowerbyella undulata* (Salter) Jones : *pars* : 452, pl. 24, figs. 4–6, *non* fig. 3.
1928 *Sowerbyella undulata* (Salter) var. *tricostata* (Reed) Jones : 458, pl. 24, figs. 8, 9.
1929 *Plectodonta duplicata* (J. de C. Sowerby) Kozlowski. : 113
1929 *Plectodonta mullochensis* (Reed) Kozlowski : 113.
1929 *Plectodonta superstes* (Jones) Kozlowski : 113.
1929 *Plectodonta* (*Eoplectodonta*) *praecursor* [*sic*] (Jones) Kozlowski : 113.
1965 *Eoplectodonta* (*Eoplectodonta*) *praecursor* [*sic*] (Jones) Williams : H380, fig. 243, 5a–c.

Diagnosis. Often large *Eoplectodonta* which are usually relatively wide, with a short median septum in the pedicle valve. Despite considerable variation within populations, most individuals have a fairly well developed median septum in the brachial valve. Many individuals possess slight *Ygerodiscus*-like undulations, and on the pedicle valve exterior there is usually a prominent central costa with two small undulations on each side of it which die away quickly anteriorly.

Description. *Exterior.* Pedicle valve very convex, semicircular in lateral profile, with a very concave brachial valve. Pedicle valve enrolled over hinge line, pedicle valve umbo incurved ; there is a concave hollow at the brachial valve umbo apart from the tiny protegular node. Outline alate to semicircular (compare Plate 5, fig. 10 with Plate 6, fig. 7 from the same population), but length seldom exceeds valve width. Maximum width hinge line, or slightly anterior in a few specimens ; very variable, even within a population, but often exceeding 20 mm. Ornament variable, normally unequally parvicostellate with about 200 costae in adult specimens and up to 15 small costellae between each costa (Plate 5, fig. 1), however in some specimens (e.g. Plate 6, figs. 10, 11) the distinction between the two types of rib breaks down, and the whole valve appears to be covered with costellae of a more or less uniform size. On pedicle valve exterior there is a stronger median costa, with two small undulations on each side which die out quickly anteriorly, usually within 2 mm of the umbo. This feature is particularly noticeable on young individuals (Plate 8, figs. 1, 2), which is why Reed was misled into giving the separate trivial name *tricostata* to such young forms. Sometimes undulate (e.g. Plate 7, figs. 1, 2), but within a population there is complete gradation between unulate and smooth specimens. Growth lines sometimes visible. Small rugae often developed in the region close to the ears. The interareas are set at an obtuse angle under the incurved pedicle valve. Oblique traces of the denticle growth tracks can be seen from the

outside of the interareas as well as the normal growth lines parallel to the hinge line. Margins of delthyrium diverge at an angle of between 90 and 110 degrees (Text-fig. 3a). No deltidial plates. Pair of small discrete chilidial plates set at a slight angle to the interarea, between which may be seen the posterior face of the cardinal process. Central shaft completely visible, also two lateral processes, the bases of which are partly hidden behind chilidial plates. Very small apical foramen sometimes visible, mostly, however, it appears to have been plugged by calcite.

Pedicle Valve Interior. Hinge line denticulate for approximately half its length, although sometimes as much as three-quarters. No real teeth, although in some specimens the central part of the hinge line projects slightly anteriorly on each side of the delthyrium, forming a very slight swell, analagous to the composite plates of some stropheodontids. Flaring away at the same angle as the sides of the open delthyrium are a pair of small dental plates fused to the valve floor acting as posterior muscle bounding ridges. Small median septum confined to the very posterior end of the valve bifurcating and then dying out posteriorly of the anterior of the muscle bounding ridges. Muscle scars strongly impressed, divergent from each other at 50 to 80 degrees. No striae on muscle field.

Vascular system often well impressed consisting of pair of main trunks running from anterior part of muscle field, which subdivide many times, but with a high degree of variability (see Text-fig. 5, also Plate 6, figs. 1, 3, 7, 8 and Plate 8 figs. 3, 4). Valve interior often highly papillate, except postero-medianly.

Brachial Valve Interior. Fossettes on the hinge line corresponding to denticles on pedicle valve. Cardinal process prominent, trifid when viewed from the posterior, with central shaft and two lateral processes, separated by grooves. Viewed from above, cardinal process bifurcates anteriorly and merges with flaring clavicular plates, not so large as *Eoplectodonta* aff. *duvalii* (Plate 12, figs. 14, 15). Median septum usually present, of variable strength, sometimes strong and running a long way anteriorly (Plate 5, fig. 4), at other times no more than the residual ridge between two callouses (Plate 5, fig. 6). Inner side septa usually strong and well-developed, growing initially perpendicular to the valve floor, then curving over laterally in larger specimens. Outer side septa variably developed, sometimes almost absent in smaller specimens (Plate 6, fig. 9), at other times massive (Plate 5, figs. 5, 11) and occasionally grotesque, with spreading tops (Plate 6, fig. 5) which are club-shaped in section. Bema also variable, invisible in young specimens except as an area without large papillae, and poorly developed in many full grown individuals (Plate 5, figs. 9, 10), but usually entire, apart from anterior interruption by the vascular system (seen well in Plate 5, figs 3, 6) ; its antero-median edge runs from anterior edges of outer side septa posteriorly to fuse with anterior edges of inner side septa to give an overall bilobed and petoloid shape to the central field. Vascular system is variable in detail, one set is seen well in the individual of Plate 5, figs. 3 and 6. Valve interior highly papillose outside the smoother central field.

Type specimens. The holotype is GSM Geol. Soc. Coll. 6874 (Plate 5, fig. 2), the original of J. de C. Sowerby (in Murchison 1839) plate 22, fig. 2. The locality label glued to the specimen reads " cefn rhyddan, Llandovery ", in Murchison's hand-

writing, although the localities given in the text (1839 : 636) are " Cefn, near Welshpool ; Robeston Wathen, Pembrokeshire ". The specimen may be definitely recognized as the original of the figure, since it is distinctively broken, and also possesses well-preserved vascular markings, both features reproduced on the plate. The grey siltstone matrix excludes Robeston Wathen, and is closer to other material from Cefn Rhyddan than from Cefn, near Welshpool, and the text locality is probably an error for Cefn Rhyddan, a small quarry in the A_4 beds of Llandovery.

Localities and material. A_4 beds (Lower Llandovery, Rhuddanian), Cefn Rhyddan quarry, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7622 3248. (GSM Geol. Soc. Coll. 6874, 6877, BB 31668) (Plate 5, figs. 1, 2).

Gasworks Mudstone (Lower Llandovery, Rhuddanian) Pembrokeshire, Wales.

(i) opposite entrance to the Gasworks, Haverfordwest, Grid Ref. SM/9588 1533. (GSM 37568, 37571–3 etc., BB 31684–31759, BB 31670–4 etc.) (Plate 5, figs. 3–12, Plate 6, figs. 1–8).

(ii) north end of railway cutting, 150 yards SW of Haverfordwest Station. Grid Ref. SM/9588 1563. (GSM 37567, GSM TCC 1191–1209, BB 32055–78) (Plate 6, figs. 9–14).

(iii) other localities listed by Jones (1928) : Frolic path, 620–625 yards from gate at Higgon's Well, Haverfordwest ; 350 yards WSW of Merlin's Bridge, Haverfordwest ; riverside 99 yards and 218 yards SE of gate at Higgon's Well, Haverfordwest ; old quarry on east side of Black Backs Bridge, 3 miles from Haverfordwest on road to Rhos, and many other localities mentioned in Strahan *et al.* 1914 : 236–7 and Cantrill *et al.* 1916 : 57.

Gasworks Sandstone (Lower Llandovery, Rhuddanian) 20 yards S of wall bounding the old work house grounds, Union Hill, Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/956 152. (GSM 37575–79, GSM Pg2722–37) (Plate 8, figs. 5–8).

Woodland Formation (Lower Llandovery, Rhuddanian), Woodland Point, south of Girvan, Ayrshire, Scotland. Grid Ref. NX/168 952 (B 73537–40, B 73749–50, BB 31830–5, BB 31949–74, BB 31984–91 etc.) (Plate 7, figs. 1–11, Plate 8, figs. 1–4).

Mulloch Hill Formation (Lower Llandovery, Rhuddanian), Mulloch Hill quarry, near Girvan, Ayrshire, Scotland. Grid Ref. NS/2703 0399. (B 44648–9, B 44718–9 etc.) (Plate 8, figs. 9–11).

Dimensions (in mm.)

	l.	w.
GSM Geol. Soc. Coll. 6874, pedicle valve internal (Plate 5, fig. 2), Cefn Rhyddan, holotype	11·6	—
GSM Geol. Soc. Coll. 6877, brachial valve external (Plate 5, fig. 1), Cefn Rhyddan	11·1	19·8
BB 31668 pedicle valve internal, Cefn Rhyddan	7·3	15·5
B 73537 pedicle valve external (plate 8, fig. 1), Woodland Point	3·2	8·5
BB 31958 pedicle valve external, Woodland Point	13·8	20·1
BB 31957 brachial valve external, Woodland Point	8·5	20·8
BB 31960 brachial valve external, Woodland Point	8·4	17·3
BB 31955 brachial valve external, Woodland Point	6·0	15·8

Discussion. Only a small population of *Eoplectodonta duplicata* is known from the type locality near Llandovery, they fall within the variation shown by the large population of approximately the same age from the Gasworks Mudstone, opposite the entrance to Haverfordwest Gasworks, Pembrokeshire, about 50 miles away. Jones (1928) named two species, *precursor*, from the Gasworks Mudstone at another locality (Plate 6, figs. 9–14), and *superstes* from the overlying Gasworks Sandstone of the same area (Plate 8, figs. 5–8). After consideration of both the type specimens and also topotypic collections of these species, they are here placed within the synonomy of *duplicata*. Kozlowski (1929) designated *precursor* (which he mis-spelt *praecursor*) as the type species of *Eoplectodonta*, and so *duplicata* now assumes this role.

In his monograph of the Girvan brachiopods, Reed (1917) erected what he described as new varieties of *Plectambonites transversalis* ; *mullochensis* from the Mulloch Hill Formation (Plate 8, figs. 9–11), which he termed Lower Llandovery, and *tricostata* from Woodland Point (Plate 7, figs. 1–11, Plate 8, figs. 1–4) which he termed Middle Llandovery. From recent collecting and field work by the present writer and Dr. P. Toghill, to be published separately, these two localities are now known to be of virtually identical age, i.e. older than at least part of the *cyphus* Zone of the Lower Llandovery (Rhuddanian). This is similar to the age of the *duplicata* type locality, and the Scottish forms fall within the range of variability of the Welsh species, thus Reed's two names are placed into the synonomy of *duplicata*.

The species, as with many other plectambonitaceans, is extremely variable. For example, the median septum is sometimes barely visible (Plate 5, figs. 3, 6) and at other times most marked (Plate 5, figs. 4, 7).

Eoplectodonta penkillensis (Reed)

(Plate 9, figs. 1–15, Plate 10, figs. 1–12, Plate 11, figs. 1–16)

1868 *Leptaena transversalis* Dalman ; Davidson : 19, pl. 3, figs. 8–13.
1871 *Leptaena transversalis* Dalman ; Davidson : 318 *pars*, pl. 48 figs. 3, 9, *non* figs. 1, 2, 4–8.
1917 *Plectambonites transversalis* (Dalman) var. *penkillensis* Reed : 888, pl. 16, figs. 3–7.
1928 *Sowerbyella penkillensis* (Reed) Jones : 443.
1928 *Sowerbyella millinensis* Jones : 444, pl. 23, figs. 13–16.
1928 *Sowerbyella millinensis* var. *parabola* Jones : 446, pl. 23, figs. 18–20.
1928 *Sowerbyella millinensis* var. *canastonensis* Jones : 447, pl. 23, figs. 17, 21–2.
1929 *Plectodonta millinensis* (Jones) Kozlowski : 113.
1945 *Plectodonta millinensis* cf. var. *canastonensis* (Jones) Lamont & Gilbert : 659, pl. 4, figs. 13–14.

Diagnosis. Smaller *Eoplectodonta* which are relatively wide, and often possess an incurved umbo with a smaller interarea than *E. transversalis*. The brachial valve median septum is usually clearly seen. Very small thin deltidal plates are present on either side of the open delthyrium.

Description. *Exterior*. Pedicle valve convex, brachial valve concave, though often less so than in other species of *Eoplectodonta*. Pedicle umbo moderately prominent and pedicle valve enrolled over hinge line. Outline alate to semicircular.

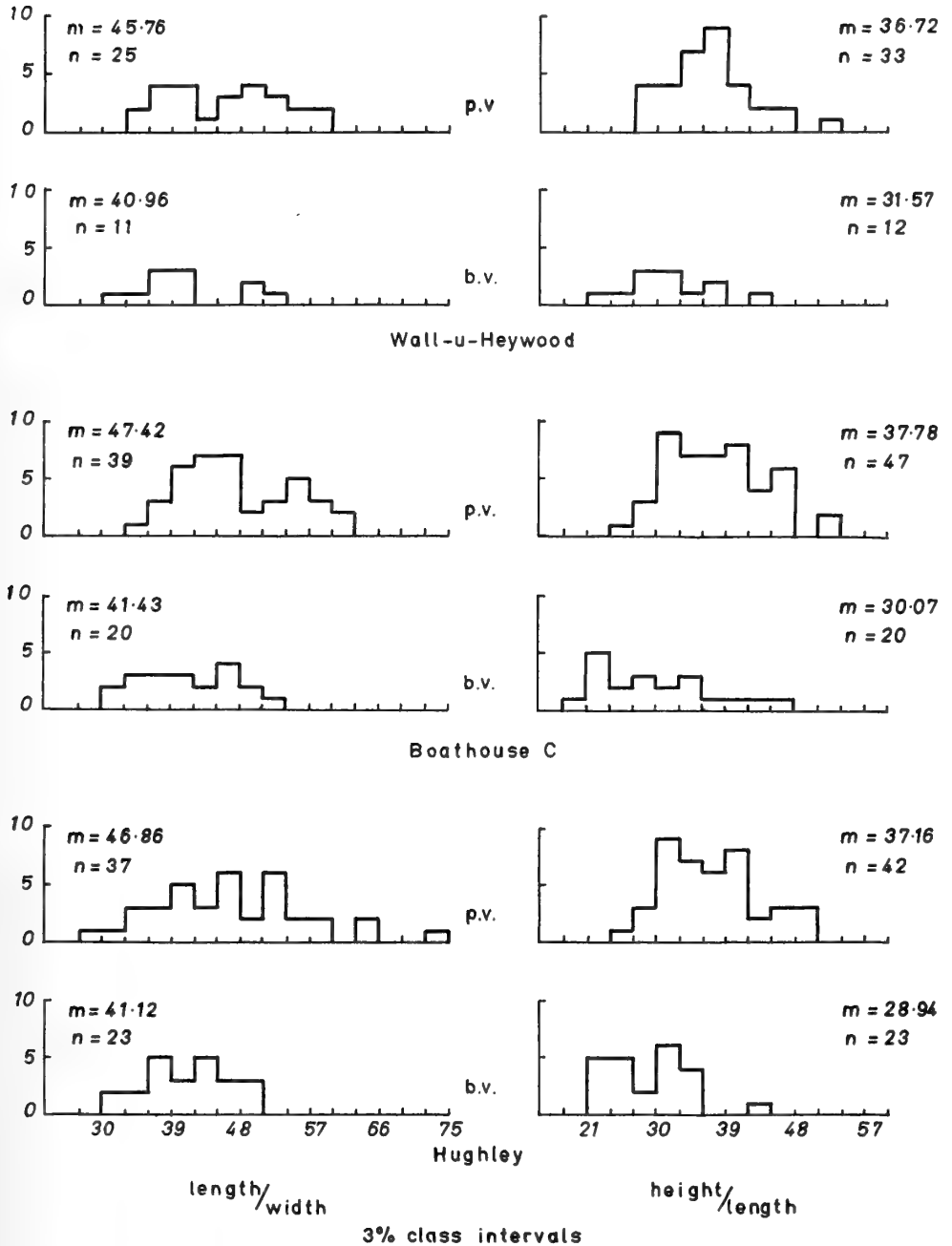

FIG. 7. Variation of *Eoplectodonta penkillensis* in three populations from the Hughley Shale (Telychian) of Shropshire, England. n = number of specimens, m = mean, p.v. and b.v. = pedicle and brachial valves. For detailed localities see text.

Maximum width at hinge line, but alae are often rounded off. Maximum width 16 mm. in over 400 specimens. Ornament unequally parvicostellate with from 8 to 22 larger costae, in between each of which are from 4 to 15 small costellae. Often a slightly stronger central median costa (Plate 11, fig. 15). In some specimens the distinction between the relative strengths of the two ribbing types tends to break down (Plate 10, fig. 7) ; there is also a large amount of variation within one population. Some individuals slightly undulate (Plate 11, figs. 4, 7) but most smooth, the undulation is not as extreme as in *Ygerodiscus* (compare with Plate 15). Small rugae often seen, confined near the hinge line (Plate 10, fig. 7, Plate 11, fig. 15). Growth lines occasionally seen, but not so prominent as on *E. transversalis*. Delthyrium open, but, unlike other species of *Eoplectodonta*, there are a pair of thin bladelike deltidial plates which protrude slightly out from the interarea (Text-fig. 3b). Chilidial plates larger than other species, although still discrete from each other ; their junction with the interarea a smooth curve rather than an angular break. Central shaft of cardinal process is visible from exterior, but bases of two lateral processes are hidden by chilidial plates. Small apical foramen sometimes visible, usually, however, it appears to have been plugged by calcite.

Pedicle Valve Interior. Hinge line denticulate for at least half its length, sometimes nearly all. No teeth but the " composite plate " swelling is again found (Plate 11, fig. 8). Small dental plates flare out anterolaterally, dying away at the side of the muscle field. Small medium septum, confined to the umbonal area, bifurcating anteriorly before merging with the valve floor. Muscle field rhomboidal in shape, with vascular system anterior to it as two long antero-laterally directed mantle canals which split up into many secondary canals more than half-way down the length of the valve. Valve interior often very papillate, except on muscle field.

Brachial Valve Interior. Fossettes along the hinge line, corresponding with pedicle valve denticles. Cardinal process less massive than in *E. duplicata*, and forming posterior wall of a deep pit which extends almost to the valve exterior. Clavicular plates diverge between 85 and 110 degrees. Median septum of variable length (on Plate 10 compare fig. 10 with fig. 12). Inner side septa usually the longest structures inside brachial valve, even in larger specimens (Plate 11, figs. 9, 13), outer side septa are not so large. There are no specimens of *E. penkillensis* on which the outer side septa reach the grotesque proportions seen in *E. duplicata*, *E. transversalis* and *E. duvalii*. Bema variably developed, not usually continuous anteriorly, it often merges with the shell floor lateral to the anterior edge of the side septa, with characteristic curved sides. Vascular system not well known. Valve interior often highly papillose (Plate 10, figs. 4, 12) outside the muscle field.

Type specimens. Lectotype (here chosen) B 44710, a partly exfoliated pedicle valve, the original of Reed 1917 plate 16, fig. 3, collected by Mrs. Gray from "Bargany Pond Burn", Girvan, Ayrshire. This locality is now known to be of Upper Llandovery (Fronian) age and is at a very small stream 200 yards SE of its junction with Lauchlan Burn. Grid Ref NX/2500 9858.

Localities and material. " Camregan Group" (formation name needs revision) (Fronian). The locality called by the Gray family "Bargany Pond Burn ",

actually a small stream which is a tributary of Lauchlan Burn, near Girvan, Ayrshire, Scotland. Grid Ref. NX/2500 9858. (Plate 11, figs 14–16) (B 44710–7 etc).

" Penkill Group " (formation name needs revision, the horizon is very similar to Bargany Pond Burn) (Fronian). The locality called by the Gray family " Penkill ", in a very small brook 550 yards SE of Penkill Castle, near Girvan, Ayrshire, Scotland. Grid. Ref. NX/2360 9832. (B 44599, B 44601, B 44632–44 etc.).

Uzmaston Beds (Telychian), 100 yards NW of Haroldston St. Issells Church, near Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9636 1409. (Plate 9, figs. 1, 2, 4, 5) (GSM 37556–9, GSM TJ929–78).

Uzmaston Beds (Telychian), near ruins of mill, 200 yards W by N of Millin Farm, 3 miles ESE of Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9943 1418. (Plate 9, figs. 8, 9, 11, 12) (GSM 37530, GSM 37540–1, BB 32419 etc.).

Canaston Beds (Telychian) road cutting opposite Canaston Farm, near Narberth, Pembrokeshire, Wales (Plate 9, figs. 3, 6, 7, 10) (GSM 37531, BB 32418 etc.).

Canaston Beds (Telychian) south bank of the eastern arm of the Cleddau, east of Haverfordwest, Pembrokeshire, Wales. Grid. Ref. SN/0485 1385. (Plate 9, figs. 13–15, Plate 10, figs. 1–3) (BB 31839, BB 32219–21, BB 32223–8 etc.)

C_5 Beds (Telychian), road cutting opposite Cefn Cerig Farm, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7746 3229. (BB 31761–31823).

Hughley Shale (late Fronian and Telychian) at the following main localities:—

(i) bank of River Onny, near Wistanstow, Shropshire, England. Grid. Ref. SO/4260 8532. (Plate 10, figs. 7–9, 11, 12) (OUM C11943–77).

(ii) south-west bank of Heath Brook, 500 yards ENE of the Plough Inn, Wall-under-Heywood, Shropshire, England. Grid Ref. SO/5120 9276. (OUM C13003–55).

(iii) stream exposure near Hughley, Shropshire, England. Grid Ref. SO/5605 9747. (Plate 11, figs. 3, 4, 7) (BB 31838, 31840, OUM C13655–735).

(iv) stream exposure 270 yards SW of the house called Domas, near Harley, Shropshire, England. Grid Ref. SJ/5936 0062. (Plate 11, figs. 1, 2) (BB 32222 etc., OUM C13541–654).

(v) stream exposure in Boathouse Coppice, east of Sheinton, Shropshire, England. Grid Ref. SJ/6205 0398. (OUM C12572–657).

Wych Beds (Telychian) bank on south side of football pitch at Cowleigh Park, Malvern Hills, Herefordshire, England. Grid Ref. SO/7616 4723. (A.M. Ziegler Collection OUM C4845–96) (Plate 11, figs. 5, 6, 8–13).

The species occurs in many other localities in the Welsh Borderland, particularly in Shropshire and Montgomeryshire.

Dimensions (in mm.)

	l.	w.
B 44710 pedicle valve, lectotype (Plate 11, fig. 14) Bargany Pond Burn.	7·4	approx. 14
B 44712 pedicle valve internal (Plate 11, fig. 16) Bargany Pond Burn.	8·2	approx. 14
B 44713 pedicle valve internal, Bargany Pond Burn	8·2	11·6
GSM 37531 (first specimen) brachial external mould (Plate 9, fig. 3) Canaston Farm.	6·5	12·1

	l.	w.
GSM 37531 (second specimen) pedicle internal mould (Plate 9, fig. 6) Canaston Farm.	7·1	approx. 12
GSM 37531 (third specimen, on other side of slab from first two) pedicle internal mould, Canaston Farm.	6·9	13·0

Discussion. In the Upper Llandovery of Britain, plectambonitaceans are abundant at many localities. They were usually referred to *Leptaena transversalis*, Reed (1917) erected *penkillensis* as a variety of that species. In 1928 Jones erected a new species, *millinensis*, with two varieties, *parabola* and *canastonensis* from Pembrokeshire, and most subsequent writers have used one or more of these last names.

Apart from the type locality of *millinensis*, an old pit now obscured, collections have been gathered from the type localities of these nominal species and subspecies, and have been considered together with other large collections, mainly from Shropshire and the Welsh Borderland. Text-fig. 7 shows the measurements of the populations at three localities in the Hughley Shale, Wall-under-Heywood, Boathouse Coppice, and near Hughley itself, and show the very large variation in the relative width, length and height. The histograms appear in some cases to have some bimodal arrangement. That this is not taxonomically significant, however, is shown by the fact that individuals from, say, the left of a trough in a height/length ratio histogram, fall quite at random into the corresponding length/width ratio histogram, and vice versa. Despite the very wide range observed, the means of the figures are very similar between the three collections, leaving no room to doubt that only one species is represented in all three cases. The relative strength, and even presence and absence, of some internal structures in the valves was also seen to possess a remarkable range of variation.

Jones originally defined his two " varieties " *parabola* and *canastonensis* (1928: 446–7) on the length/width-proportions, *parabola* being longer and less wide than *canastonensis*. Collections from the two type localities gave the following measurements :

S. millinensis parabola (near old mill, 200 yds W by N of Millin Farm 3 miles ESE of Haverfordwest, Pembrokeshire).

$\bar{l}/\bar{w}$ for 20 pedicle valves 44·9% (OR 33·7–63·4%), $s^2 = 84·6$

$\bar{l}/\bar{w}$ for 27 brachial valves 44·3% (OR 35·7–57·9%), $s^2 = 39·1$

S. millinensis canastonensis (road opposite Canaston Farm, 2½ miles W. of Narberth, Pembrokeshire).

$\bar{l}/\bar{w}$ for 5 pedicle valves 49·0 (OR 38·3–62·7), $s^2 = 85·5$

$\bar{l}/\bar{w}$ for 12 brachial valves 46·8 (OR 35·8–59·8), $s^2 = 46·1$

When significance tests, (in this case ' t ' tests) are applied, the differences between the two collections are insignificant, and on the basis of length/width ratios the two " varieties " cannot be considered separable, even as subspecies. It is unfortunate that *penkillensis* was not well known (the brachial interior was not figured by Reed) at the time of Jones' work as he (1928 : 443) noted that " it bears a considerable resemblance to certain forms which occur abundantly in the Millin Stage of Haverfordwest and Narberth, it is probable that the internal features are also of the same type ".

However, despite the exceptionally wide variability shown by the various species of *Eoplectodonta*, the length/width and height/length ratios of *E. penkillensis* are significantly lower than those of *E. transversalis* (Text-fig. 9). In other words *E. penkillensis* is relatively wider, but less curved, than the contemporary Scandinavian species.

The form described by Davidson (1868, 1873) ; as *L. transversalis*, which occurs in such numbers in the Pentland Hills may also be referred to *penkillensis*. Lamont (1947 : 200) discusses the identification of this form without conclusion apart from suggesting that a number of different forms may exist. Collections, as well as the specimens in the Davidson collection, from three Pentland localities indicate that only one species is present, and that this falls within the range of *penkillensis* from both Scotland and Shropshire. The age of the Pentland beds is very probably *crenulata* Zone of the Telychian, although there is a slight possibility that they could extend into the lowermost Wenlock.

The lower part of the range of *E. penkillensis* is not fully documented. Forms from the Middle Llandovery (Idwian) of the Llandovery area may be referred to the species, as can the roughly contemporary population at Newlands, Girvan. Nothing earlier is yet known, but the range of variability of all species of *Eoplectodonta* is such that some specimens of *E. penkillensis* are similar to small forms of *E. duplicata*, and there seems to be no need to look further than the latter species for a possible ancestor.

Eoplectodonta transversalis (Wahlenberg)

(Plate 12, figs. 1–13)

1819 *Anomites transversalis* Wahlenberg : 64.
1828 *Leptaena transversalis* (Wahlenberg) Dalman : 109, pl. 1, fig 4.
non 1871 *Leptaena transversalis* (Wahlenberg) ; Davidson : 318, pl. 48, figs. 1–9.
? 1894 *Plectambonites transversalis* (Dalman) Hall & Clarke ; 295, pl. 15, figs. 34–6.
non 1916 *Plectambonites transversalis* (Wahlenberg) ; Holtedahl : 83, pl. 15, figs. 1–4.
non 1917 *Plectambonites transversalis* (Dalman) ; Reed : 886, pl. 15, figs. 35, 36.
non 1928 *Sowerbyella transversalis* (Davidson), pars [Wahl. ?] Jones : 448, pl. 23, fig. 23, pl. 24, fig. 1.
1929 *Plectodonta transversalis* (Dalman) Kozlowski : 113.
1967 *Ygera transversalis* (Wahlenberg) Havlíček : 58.

Diagnosis. Smaller *Eoplectodonta* with a lower length/width ratio, a less incurved umbo and larger interarea, and finer brachial valve septa than most other species.

Description. *Exterior.* Pedicle valve convex, maximum convexity near valve apex and decreasing anteriorly, with brachial valve concave. Pedicle umbo prominent, pedicle valve very enrolled over hinge line, so that interarea more visible when viewed from above as compared with other species (see Plate 12, figs. 3, 9 and 11 ; compare these with the more enrolled pedicle valve and smaller interarea of *Eoplectodonta duvalii* on the same plate, fig. 16). Outline semicircular to semi-oval, with length often approaching width. However small specimens often quite alate ; the growth sequence is first one of increasing width and finally one of increasing length

(shown by the growth lines on the neotype, Plate 12, figs. 1–3). Size of adult specimens small for *Eoplectodonta* ; maximum width 14 mm. in a population of more than 300 specimens. Ornament unequally parvicostellate with 12–30 larger ribs (depending mainly on length of specimen) some of which arise by intercalation anteriorly (Plate 12, fig. 11). Between 5 and 11 fine costellae between each large rib, some so fine as to to be almost invisible, appearing merely as rows of pseudopunctae through the translucent shell. Growth lines often prominent over valve surface, occasionally showing tendency to be lamellar. Small rugae seen only rarely, confined to the area

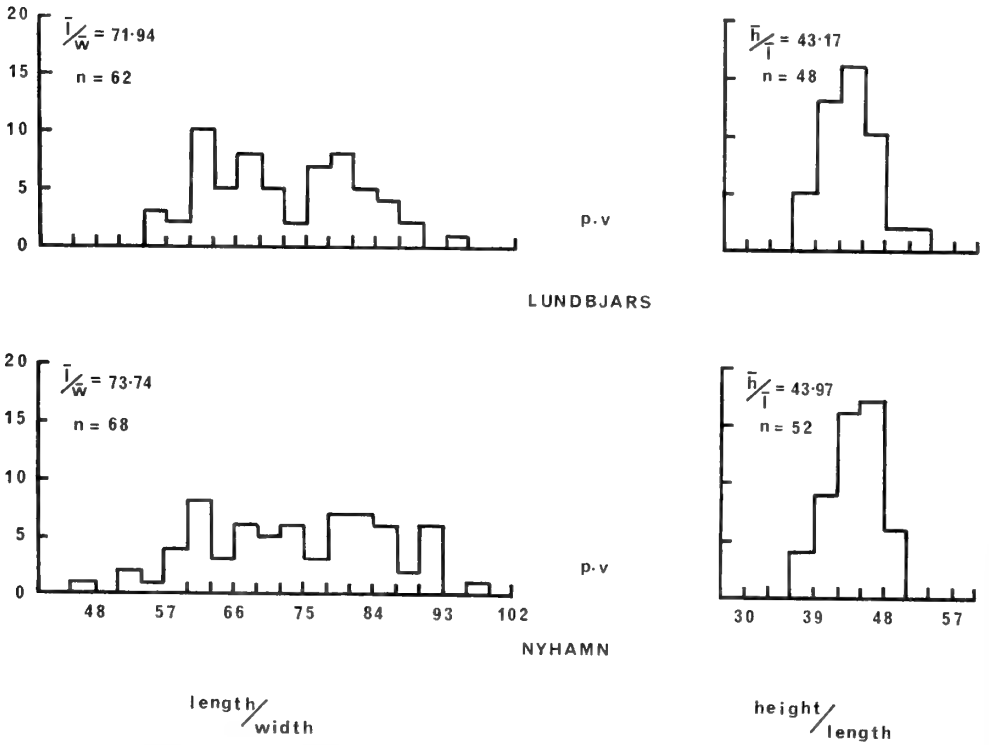

FIG. 8. Variation of *Eoplectodonta transversalis* in two populations from the Lower Visby Marl (Telychian) of Gotland, Sweden. Abbreviations as in Text-fig. 7. Bottom axis percentages with 3% class intervals.

near the alae. Interareas relatively large for the genus, at a shallow angle to each other. Oblique denticle growth tracks can be seen through the translucent shell. Delthyrium with sides sometimes straight and sometimes curved, diverging between 90 and 105 degrees. On either side are a pair of almost vestigial deltidial plates. Small discrete chilidial plates between which can be seen the cardinal process shaft and sometimes the two lateral processes (Text-fig. 3c). Small apical foramen occasionally seen, but often plugged by calcite.

Pedicle Valve Interior. Hinge line denticulate from between half and nearly all its length, with large denticles set oblique (Plate 12, figs. 10, 12, 13). Denticle length often irregular ; they protrude anteriorly slightly more on each side of the delthyrium, analagous with the stropheodontid composite plate. Dental plates fused to the edge of the delthyrum, flaring anterolaterally, continuing as muscle bounding ridges dying out anteriorly to fuse with the valve floor (seen in oblique view in Plate 12 fig. 12). Short median septum in the posterior part of valve, bifurcating, then merging with valve floor. Muscle field is similar to *Eoplectodonta duplicata*, described above in section on morphology (text-fig. 2). Vascular system (Plate 12 fig. 10) consisting of two main canals bifurcating near anterior margin, the two branches giving off many secondary branches. Valve interior is highly papillate, more than other species of *Eoplectodonta*, apart from the smooth central field.

Brachial Valve Interior. Hinge line has small fossettes to accommodate pedicle valve denticles. Cardinal process prominent, apparently fused posteriorly to the pair of chilidial plates. Pit in front of the cardinal process very deep, extending nearly to the valve exterior under the apical node. Thus the cardinal process appears a hollow structure, in contrast to the more massive deposits of secondary calcite found in *E. duvalii* (compare Plate 12 fig. 4 with Plate 12 fig. 14). Clavicular plates flaring anterolaterally, relatively short and spikey. Median septum variably developed ; never as strong as side septa, sometimes only developed anteriorly (Plate 12 fig. 4), sometimes for most of the valve length (Plate 12 fig. 7). Inner side septa prominent, nearly reaching pedicle valve when the valves are shut, apart from posteriorly where there is a well developed geniculation to accommodate the body cavity. These septa usually thicker at top than base, but tops not as thick as those of outer side septa in adults. Outer side septa smaller than inner in young, but grow larger and often end up larger than inner side septa. The relationship of the two pairs of septa also varies ; in some specimens (Plate 12 fig. 7) the two pairs join anteriorly, in other specimens (Plate 12 fig. 6) the inner pair wrap over the top of the outer pair, whilst in yet other specimens (Plate 12 fig. 4) the inner side septa curve round anteriorly becoming continuous with the bema enclosing the outer side septa. Bema emerges from behind clavicular plates in an anterolateral direction curving round first directly anteriorly, then antero-medianly, sometimes to die out, at other times merging with inner side septa. Bema sometimes more elevated off valve floor than other species of *Eoplectodonta*. Vascular canal system not well developed. Papillae very coarse (outside the muscle field) compared with *Eoplectodonta penkillensis*.

Type specimens. The original material of Wahlenberg has been lost, probably by incorporation into large poorly labelled general collections (Dr. A. Martinsson has kindly searched the collection at Uppsala on my behalf). The originals of Dalman's figures are also unidentifiable in the Dalman Collection at Naturhistoriska Riksmuseum, Stockholm. Dalman's figures are stylised views of complete specimens, whibh are in any case difficult to identify with particular individuals. The material in the Riksmuseet is poorly localized, except to identify the original horizon of *transversalis* as the Lower Visby Marl of Gotland. Thus I have selected a neotype from my own collection and given it to Naturhistoriska Riksmuseum, registered

number RMS Br 102394 (Plate 12, figs. 1–3). The locality is Lower Visby Marl, freshly weathering out at base of cliff at beach exposure 1 km W. of Lundbjars, 800 m. N of Nyhamn, Gotland. Swedish Grid reference CK/465 062.

Localities and material. Lower Visby Marl (Upper Telychian), Gotland, Sweden.

(i) marl weathering out from base of cliff, 1 km west of Lundbjars, and 800 m north of Nyhamn. Swedish Grid Ref. CK/465 062. (Plate 12, figs. 1–5, 8, 11–13) (RMS Br 102394, BB 32420–4, BB 32857–61 etc.).

(ii) marl weathering out of foreshore exposure, 200 m north of Nyhamn. Swedish Grid Ref. CK/463 055. (Plate 12, figs. 6, 7, 9, 10) (BB 32425–8 etc.).

(iii) other localities on NW coast of Gotland where the valves may be found loose on the foreshore include Norderstrand, Snäckgärdsbaden and Irevik.

Dimensions (in mm.)

	l.	w.	h.
All specimens from Lundbjars			
RMS Br 102394, conjoined valves, neotype (Plate 12, figs. 1–3)	10·6	approx. 13	4·7
BB 32422, conjoined valves (Plate 12, fig. 11)	10·5	13·4	4·7
BB 32857, conjoined valves	11·2	11·8	5·0
BB 32858, conjoined valves	7·4	10·9	3·2
BB 32859, conjoined valves	6·5	9·2	2·5
BB 32860, conjoined valves	6·5	10·9	2·9
BB 32861, conjoined valves	5·7	8·1	2·2

Discussion. With the doubtful exception of some figures of American material from the Niagara Group at Lockport by Hall & Clarke (1894), *Eoplectodonta transversalis* has not been authentically illustrated since the classic paper by Dalman (1828), who provided the first pictures of the species which Wahlenberg had erected without figures in 1819.

There can be no doubt from Dalman's figures of *transversalis* that they represent the *Eoplectodonta* which may be found in such numbers in the lower Visby Marl of Gotland, Sweden. This form has a significantly lower and more constant length-width ratio than its contemporary British species *penkillensis* (Text-fig. 9), caused not so much by initial differences as by differential growth along the length axis rather than the width.

The species of *Eoplectodonta* from Gotland are in some need of review. In his many admirable stratigraphical works, culminating in his guide to the International Geological Congress (1960), Hede lists the following (all of which he referred to *Plectodonta*). " *transversalis* (Dalman) " from the Lower Visby Marl ; "*transversalis lata* (Jones) " from the Upper Visby Marl and Slite Group and " cf. *duvali* (Davidson) " from the Högklint Beds. Hede is correct in the separation of the different forms which occur on Gotland, but was without the type English material for reference. It is now known that in England *lata* is a junior synonym of *duvalii* (see below). However there is in the Upper Visby Marl of Gotland a very large and wide form of *Eoplectodonta* which does not seem to be found elsewhere. This form (Plate 13,

fig. 1) is relatively rare, and at such rich localities as Kneippbyn, I was not able to procure a good enough sample to warrant full description. There is such a sample in the Naturhistoriska Riksmuseum, Stockholm (Br 31330–96), but it is without locality. There is no doubt that this material is specifically distinct from *transversalis*, but its relationship with genuine *duvalii* populations is less easy to estimate. English *duvalii* is not so large (some of the Gotland material is over 28 mm. wide).

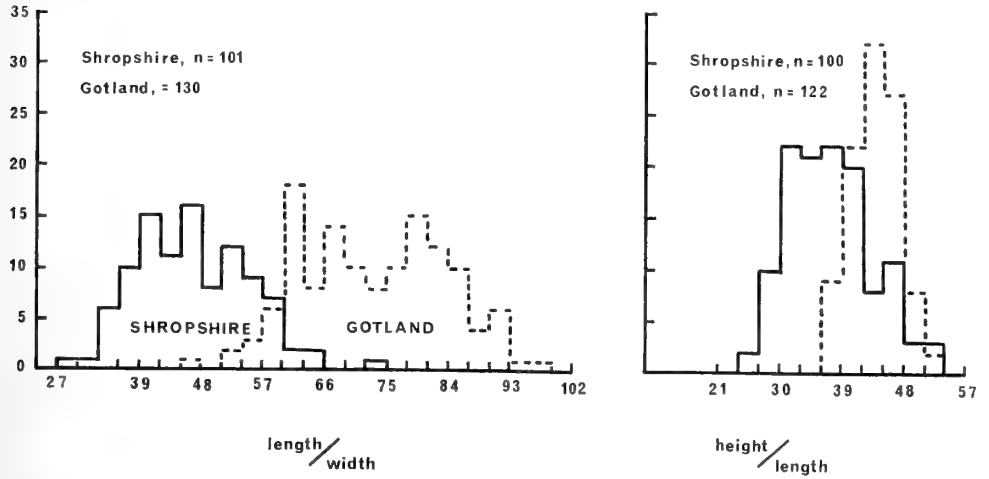

FIG. 9. The pedicle valves of *Eoplectodonta transversalis* from Gotland compared with *E. penkillensis* from Shropshire. Data summed from Text-figs. 7 and 8. Bottom axis percentages with 3% class intervals.

The extra size is made up, however, not by an overall increase, but in a larger proportion of shell material outside the bema, so that the central septal region remains similar in size to large *duvalii* and thus appears small in relation to the rest of the shell. To name this form would be premature on the evidence at present available ; perhaps a new subspecies of *duvalii* would be most apt, hence the title of *Eoplectodonta* aff. *duvalii* to the figured specimen. What Hede refers to as *transversalis lata* from the Slite Beds (Plate 12, figs. 14–16) and as " cf. *duvali* " from the Högklint, may be referred to *Eoplectodonta duvalii sensu stricto*, described below.

Thus, although *transversalis* has probably been the most widely quoted sowerbyellid species, particularly by stratigraphers, it appears to be confined to one formation, the Lower Visby Marl of Gotland, of uppermost Llandovery (high Telychian) age. However it is possible that the species could also have occurred outside Europe.

Two large populations were recovered from existing outcrops on Gotland, at Lundbjars and Nyhamn. The fossil is also very common at many other places along the north-west coast of Gotland, but very often, as at the classic localities of " Visby " and " Norderstrand " the specimens form part of the beach shingle, weathered out from outcrops just below the wave line (there is almost no tide in that part of the Baltic).

Eoplectodonta duvalii (Davidson)

(Plate 12, figs. 14–16, Plate 13, figs. 3, 7, 10)

1847 *Leptaena transversalis* Dalman ; Davidson : 57, pl. 12, figs. 17–19.
1847 *Leptaena duvalii* Davidson : 58, pl. 12, figs. 20, 21.
1848 *Leptaena duvalii* Davidson ; Davidson : 317, pl. 3, fig. 7.
1848 *Leptaena transversalis* Dalman ; Davidson : 318, pl. 3, fig. 10.
1871 *Leptaena transversalis* Wahlenberg ; Davidson : 318 *pars*, pl. 48, figs. 1, 2, 4–6, ? figs. 7, 8, *non* figs. 3, 9.
non 1917 *Plectambonites transversalis* (Dalman) var. *duvali* (Davidson) Reed : 887, pl. 15, figs. 37–40.
1928 *Sowerbyella transversalis* (Davidson), *pars* [Wahl. ?] Jones 488, pl. 23, fig. 23, pl. 24, fig. 1.
1928 *Sowerbyella transversalis* var. *lata* Jones : 450, pl. 420 24, fig. 2.
1928 *Sowerbyella duvali* (Davidson) Jones : 451.
1954 *Sowerbyella transversalis* var. *lata* Jones : Nikiforova : 76, pl. 7, figs. 1–2.
1960 *Plectodonta transversalis lata* (Jones) Hede ; 73, 76.
1967 *Ygera lata* (Jones) Havlíček : 58.
1967 *Ygera transversalis* (Wahlenberg) Havlíček : 58 *pars*.

Diagnosis. Larger *Eoplectodonta* with up to 33 larger ribs, relatively small interareas and incurved pedicle umbo. A median septum is present in the brachial valve, but may be nearly obscured by secondary calcite.

Description. *Exterior*. Brachial valve concave and pedicle valve convex, but not usually so much as *E. transversalis*. Umbo fairly incurved and pedicle valve enrolled over hinge line. Shape alate and semicircular to semi-oval. Maximum width (23 mm in 50 specimens) at hinge line. Ornament unequally parvicostellate with a relatively large number of large ribs (33 counted in one specimen), with between 4 and 10 fine secondary costellae between each. Large undulations rare, although many specimens possess slight undulation (Plate 14 fig. 3). Growth lines sometimes seen, not as commonly or prominently as on *E. transversalis*. Small rugae often seen near the hinge line (Plate 13 fig. 10). Interareas set at an angle to each other which is sometimes acute and sometimes obtuse, but more of an angle than in *E. transversalis* and in general more than in *E. penkillensis*. Delthyrium open, the small deltidial plates of *E. penkillensis* apparently absent. In one population from the Buildwas Beds in the Davidson Collection (from Maw's washings—all registered B 1587) there is variation between forms with small discrete chilidial plates (as found in *duplicate*, *penkillensis* and *transversalis*) and forms in which the two plates have united to form an entire chilidium. Cardinal process, of central shaft and two lateral processes, visible from exterior through the open delthyrium (Text-fig. 3d and e). Small apical foramen visible in some specimens, often plugged by calcite.

Pedicle Valve Interior. The material of this valve showing the interior is poor. Hinge line denticulate for half or more of its length. Small median septum confined to umbonal area, bifurcating anteriorly before merging with valve floor. No teeth, but small dental plates flare away antero-laterally before merging with valve floor at side of muscle field. Vascular system unknown ; valve interior often papillose except on muscle field.

Brachial Valve Interior. In contrast with the pedicle valve good material has been available. Hinge line has fossettes for half or more of its length, some specimens entirely denticulate. Cardinal process roughly the same plane as anterior commissure, jutting posteriorly of the hinge line. Cardinal process supported only from the sides, anterior of process is a deep hollow extending very nearly to valve exterior. Antero-laterally of cardinal process are flaring clavicular plates (Text-fig. 2, Plate 12, fig. 15), with rounded anterior ends, raised up from the valve floor in a mound except medianly where they merge together with the posterior ends of the inner side septa to form a central elevated area of secondary shell. Median septum usually present, but very weak, almost vestigial in larger specimens, obscured by the growth of inner side septa (Plate 12 fig. 14). Inner side septa with geniculation near the umbo, curving outwards from valve floor, ending nearly at floor of pedicle valve. Outer side septa straight at their bases, but variably curved higher up, at their posterior end outwards, at their anterior end inwards. Bema variably developed, curving round nearly meeting anterior septa in the petaloid field. Vascular system not known. Large papillae outside central field.

Holotype. B 13730 from a calcareous band in the Wenlock Shale of Walsall (Plate 13 fig. 10). The specimen was collected by Mr. Lewis, who gave it to Davidson before 1847.

Dimensions (in mm.)

	l.	w.	h.
B 13730, pedicle valve, holotype (Plate 13, fig. 10)	—	16·8	—
GSM 12697, conjoined valves (Plate 13, fig. 7)	13·4	21·5	6·3
BB 50420, conjoined valves	11·3	approx. 17	5·2
B 34846, conjoined valves	13·2	21·2	6·6
B 23171, conjoined valves	10·4	approx. 20	4·2
B 8915, conjoined valves	10·0	15·0	4·8

B 13730 and BB 50420 are from Wenlock Shales of Daw End, Walsall, GSM 12697 is from Buildwas Beds at Buildwas and the last three specimens are from the Wenlock Limestone of Dudley.

Discussion. *Eoplectodonta duvalii* has been constantly misidentified. Davidson (1847) erected the species on a specimen which has its anterior part concealed by matrix (Plate 13 fig. 10). Thus it has the appearance of being a very transverse form in Davidson's original drawing—a drawing which was repeated both in his French paper (1848) and also in his much-used monograph (1871, pl. 48, fig. 5). As a result the name *transversalis* from Gotland was used for the common *Eoplectodonta* found in the Wenlock of England and elsewhere. Jones (1928 : 448) was at the disadvantage of not having much Swedish material and followed Davidson's mistaken interpretation of *transversalis*. Jones also erected the variety *lata* for specimens of larger size and smaller length/width ratio. However he states (1928 : 450) that " these characters [of *lata*] have been observed in forms from many localities, where they occur in association with normal types ". The holotype of Jones's variety (GSM 12697, Plate 13, fig. 7) although it is a large specimen, has a normal

length/width ratio of 62%, falling within the variation of *E. duvalii* ; thus Jones's variety is here placed into synonomy and not treated as a valid subspecies.

A fuller treatment of the distribution of *E. duvalii* in England, together with locality details, will be given by Dr. M. G. Bassett in his forthcoming monograph.

As discussed above, there is an *Eoplectodonta* in the Upper Visby Marl of Gotland (Plate 13 fig. 1) which may be a subspecies of *duvalii*, but it has not been formally described here. *E. duvalii* s.s. also occurs in Gotland, in particular the Slite Marl (Plate 12 figs. 14–16).

The relationship between *E duvalii* and *E. sowerbyana* (Barrande), from the Wenlock Litěn Beds of Bohemia is difficult to assess, particularly since the Czech material occurs only as moulds in a tuff, so that ornamental details are obscure, though the vascular system is well developed (Havlíček 1967, pl. 7). Certainly the relative emphasis of internal details (Plate 13, figs. 2, 4–6, 8, 9) differs from typical specimens of *E. duvalii*, but the full range of variation of the latter is not yet definitively known, and the taxonomic identity of *sowerbyana* remains obscure, although the species may definitely be included within *Eoplectodonta*.

The form from the Kitaigorod Formation of Podolia, described by Nikiforova (1954) may also be ascribed to *Eoplectodonta duvalii* (Plate 13 fig. 3). From material collected by Dr. P. T. Warren and Dr. J. Shirley in 1968, this formation may be referred to the Wenlock Series, rather than the Llandovery. Previous support for a Llandovery age is the record of *Pentamerus oblongus* (J. de C. Sowerby), confined to Llandovery rocks of Lower Telychian (C_4) age or older. However the large pentamerids present are not *P. oblongus* but a species of *Pentamerus* which continues throughout the Wenlock, occurring rarely even in the Wenlock Limestone of Dudley (BB 31279).

Ygerodiscus Havlíček 1967

1967 *Ygerodiscus* Havlíček : 62.

Type species. *Leptaena transversalis* var. *undulata* Salter 1848.

Discussion. As mentioned in the discussion of the subfamily, populations of plectambonitaceans had a variable tendency for their shells to become buckled. Often this tendency was phenotypic, but in the Lower Silurian there are a group of populations, descendants of *Eoplectodonta*, in which buckling is invariably present, and which are also specifically distinct from contemporary unbuckled *Eoplectodonta*. Havlíček (1967) has coined the generic term of *Ygerodiscus* for these forms, and this will also be used here, despite the possibility that these species should be included in *Eoplectodonta*. One of the most compelling reasons for the distinct treatment of the two genera was the discovery, in the population of *Ygerodiscus undulatus* from Meifod, of common small *Ygerodiscus* associated with a few large specimens of *Eoplectodonta*, indicating that by the Middle Llandovery the differences had probably become truly genetic.

The following species are attributed to the genus:—

Leptaena transversalis var. *undulata* Salter 1848 (synonyms *Sowerbyella undulata*

var. *maccoyi* Jones 1928. *Sowerbyella plicata* Jones 1928, and *Sowerbyella compressa* Jones 1928).

Ygerodiscus novemcostatus Havlíček 1967, Wenlock Liteň Formation of Bohemia.

Plectambonites striatacostatus Twenhofel 1928, Llandovery Gun River and Jupiter Formations of Anticosti.

Plectodonta propinqua Rybnikova 1967, Llandovery boreholes in Latvia.

In addition *Leptaena segmentum* var. *cornuta* Davidson 1883 is doubtfully included within *Ygerodiscus* (see below).

Ygerodiscus undulatus (Salter)

(Plate 14, figs. 3–12, Plate 15, figs. 1–12)

1848 *Leptaena transversalis* var. *undulata* Salter *in* Phillips : 372.
1852 *Leptaena quinquecostata* (M'Coy) pl. iH, figs. 30, 31, 31a.
1866 *Leptaena transversalis* (Dalman) var. *undulata* Salter ; Salter *in* Ramsay : 267.
1871 *Leptaena transversalis* (Wahlenberg) ; Davidson : 320, *pars*, *non* pl. 48, figs. 1–9.
1873 *Leptaena transversalis* (Dalman) var. *undulata* Salter; Salter : 64, 82.
1928 *Sowerbyella undulata* (Salter) Jones : 452 *pars*, pl. 24, fig. 3, *non* figs. 4–6.
1928 *Sowerbyella undulata* var. *maccoyi* Jones : 457, pl. 24, fig. 7.
1928 *Sowerbyella plicata* Jones : 459, pl. 24, figs. 10, 11.
1928 *Sowerbyella compressa* Jones : 460, pl. 24, figs. 12, 13.
1951 *Sowerbyella undulata* (Salter) ; Williams : 130.
1951 *Sowerbyella undulata maccoyi* Jones ; Williams : 130.
1967 *Sowerbyella undulata* (Salter) : Rybnikova : 187, pl. 18, figs. 11–13.
1967 *Ygerodiscus undulatus* (Salter) Havlíček : 62.
1967 *Ygerodiscus undulatus maccoyi* (Jones) Havlíček : 62.
1967 *Ygerodiscus compressus* (Jones) Havlíček : 62.
1967 *Ygerodiscus plicatus* (Jones) Havlíček : 62.

Diagnosis. *Ygerodiscus* with interior arrangement very close to *Eoplectodonta*, number and strength of plicae variable. Small size, with average width of about 10 mm.

Description. *Exterior.* Pedicle valve convex, often more than a semicircle in profile, with concave brachial valve. Incurvature of umbo and enrollment of pedicle valve over hinge line variable but often strong. Outline semicircular and alate. Size is small for family—maximum width of 16·1 mm. in 140 specimens. Ornament unequally parvicostellate with between 7 and 18 larger ribs, between each from 6 to 12 very fine costellae. Coincident with the 5 to 12 central large ribs is a series of undulations, with the primary rib at the crest of the undulation in the pedicle valve and in the trough in the brachial valve. Two small undulations variably occurring on either side of the median rib in both valves (Plate 15, fig. 2), dying away anteriorly just past the umbo, these are also diagnostic of *Eoplectodonta duplicata*. Growth lines occasionally seen (Plate 14, fig. 4). Small rugae sometimes developed, confined to hinge area and alae. Interarea of the pedicle valve wider than brachial valve, the interareas at an obtuse angle. Delthyrium has pair of small, discrete, triangular chilidial plates. Shaft of the cardinal process visible along its length, the two lateral processes seen above the chilidial plates. Small apical foramen occasionally seen, but usually plugged by calcite.

Pedicle Valve Interior. Hinge line denticulate from between a quarter and three-

quarters of its length. No teeth, but small pair of antero-laterally directed dental plates at a continuation of angle of delthyrium sides. Plates die out quickly anteriorly. Muscle system similar to *Eoplectodonta*. Small thin median septum confined to umbonal area bifurcating before merging with the valve floor. Vascular markings often well developed ; two main trunks running anteriorly from under the muscle field some way to the valve margin (plate 15, figs. 1, 7, 8), before dividing laterally. Prominent papillae often developed near alae and round anterior valve margin (Plate 15, fig. 8).

Brachial Valve Interior. Hinge line fossettes correspond with pedicle valve denticles. Cardinal process trifid, supported from sides, forming the posterior wall to hollow extending nearly to valve exterior. Prominent clavicular plates, varying within one population from blade-like to squat and triangular. Median septum well developed, running from near the valve umbo for about three-quarters the length of the valve. Inner side septa prominent, their tops geniculate in profile near the valve umbo. Sometimes these septa split into two parts anteriorly (Plate 14, figs. 6, 11), but groove between these two parts does not get near the valve floor. Outer side septa present, but not so strong, and as little as half length of inner side septa. Bema usually well developed, sometimes raised much off the valve floor. Muscle system similar to *Eoplectodonta*. Vascular system poorly known. Very coarse papillae sometimes present, particularly towards valve ears and anterior margin (Plate 14, fig. 6).

Type specimen. The lectotype, chosen by Jones (1928 : 455–6) is SMA 11307 (previously registered as a/198), a mould of the exterior of a brachial valve (Plate 15, fig. 5). It is one of M'Coy's original specimens, and comes from the " Bala Schists of Mathyrafal ", and has the label " Math " stuck to it in M'Coy's writing. The locality is discussed below.

Localities and material. V_2c horizon (late Rhuddanian or Idwian), bank of River Banwy, near Meifod, Montgomeryshire, Wales. Grid Ref. SJ/1327 1057 (Plate 15, figs. 1, 4, 7–9), figs. 2 and 5 come from this or a very similar locality) (SMA 11307–8, BB 31669, BB 31903–28).

Rosemarket Beds (Idwian or early Fronian), old quarry 700 yards S of Bullford, near Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9218 0980. (Plate 14, figs. 3–9, 11, Plate 15, figs. 6, 10–12) (GSM 37560–3, GSM OJT 1000–1104, BB 32081–4 etc.).

C_1 Beds (Fronian), " near footbridge " (now disappeared) over River Sefin, south of Lletty'rhyddod, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7418 2817 (Plate 14, figs. 10, 12) (BB 32417 etc.).

B Beds (Idwian) exposure on forestry track, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/8344 3726. (Plate 15, fig. 3)(BB 32109 etc.).

B_3 Beds (Idwian), small disused quarry by roadside, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/760 309 (BB 32085–7, 32094 etc.).

Williams (1951 : 130) lists the species as occurring in all horizons in the Llandovery area between A_2 and C_{2-3} beds inclusive. I would treat at least the A_2 and A_3 populations as variants of *Eoplectodonta duplicata*.

DIMENSIONS (in mm.)

		l.	w.
All specimens from Meifod			
SMA 11307 brachial valve exterior, lectotype	(Plate 15, fig. 5)	5·9	16·1
SMA 11308 ,, ,, ,,	(Plate 15, fig. 2)	6·0	approx. 12
BB 31928 ,, ,, ,,		4·5	11·0
BB 31904 pedicle valve interior		4·8	approx. 12
BB 31909 ,, ,, ,,		3·5	7·3
BB 31913 ,, ,, ,,		5·5	13·2
BB 31910 ,, ,, ,,		7·3	10·0

DISCUSSION. M'Coy figured the holotype (1852 pl. iH, fig. 30) as "*Leptaena quinquecostata* (M'Coy), transverse variety with additional lateral ridges". This figure was quoted by Salter (*in* Ramsay 1866) as *Leptaena transversalis* Dalman var. *undulata* Salter, and the individual specimen appears in Salter's type catalogue of 1873. In addition M'Coy figured (1852, pl. iH, figs. 31, 31a) a second specimen (SMA 11308) from the same locality, which was subsequently chosen by Jones (1928 : 457) as the type of his new variety *maccoyi*. The differences between the two specimens, both natural casts of externals of brachial valves, are due to normal variation at the locality. Mathyrafal is the name of a ruined castle (spelt Mathrafal on Ordnance Survey maps) situated on the land of Upper Hall Farm, 2 miles S.W. of Meifod in Montgomeryshire. M'Coy's locality was almost certainly in the section of the Llandovery exposed in the bank of the River Banwy, about 200 yards south of the castle site. A comparative collection which contained *Ygerodiscus undulatus* was made from the river bank at Grid Ref. SJ/1327 1057 which must be at, or very near, the type locality. This area has been described by King, who gives a geological section along the river bank (1928 : fig. 2). The type locality lies in King's V_2c beds which he considered to be Middle Llandovery or even Low Upper Llandovery in age. However, recent work by Dr. J. T. Temple (1970, in press), as well as collecting by the present author, indicates that this horizon is at least partly late Lower Llandovery in age, although the Middle Llandovery may also be present.

The type specimens of *Sowerbyella plicata* and *Sowerbyella compressa* both come from the same small quarry in Pembrokeshire, and an examination and measurement of O. T. Jones's original collection, leaves no doubt that the few specimens which he labelled *compressa* are oblique to the bedding plane, and distorted specimens of *plicata*.

The age of this locality requires discussion. The Rosemarket Beds outcrop as a strip just over nine miles long, to the south of, and unconformable upon, the Pre-Cambrian Johnston Series in Pembrokeshire, Wales. The Geological Survey (Strahan *et al.* 1914, Cantrill *et al.* 1916) mapped the beds as a lower conglomerate and an upper mudstone, more than 1000 feet thick. The type locality of *plicata* is on the Milford Haven Sheet, a small farm quarry now filled with refuse. However loose blocks within ten yards of the quarry have an identical lithology, a light brown fine sandstone, to that of the type material. (There are no glacial deposits in the immediate area.) The collection contained the following brachiopods :—*Pentamerus*

oblongus (J. de C. Sowerby), *Ygerodiscus " plicatus* (Jones) ", *Coolinia* aff. *applanata* (Salter), *Clorinda* sp., *Protatrypa* sp. and an indeterminable rhynchonellid. There were also the corals *Halysites* sp., and " *Petraia* " sp. and at least two species of decalcified polyzoa. *Pentamerus* is unknown before the Middle Llandovery, but does not reach its acme until the Fronian, before evolving into *Pentameroides* in the Telychian. *Protatrypa* evolved into *Atrypa* during the Fronian. Subsequently a re-examination of the Geological Survey collection from the locality revealed a graptolite hitherto overlooked. Although poorly preserved, the specimen [on GSM OTJ 1045] has been kindly identified by Dr. P. Toghill as probably *Glyptograptus tamariscus*, unidentifiable as to subspecies, but one of the narrow forms which occur between the *cyphus* and *sedgwickii*-Zones inclusive. Thus the type locality of *Ygerodiscus plicatus* may be taken to be of Idwian (Middle Llandovery) or perhaps early Fronian age. The area as a whole needs revision ; for example a collection from the old quarry at the south end of the lane leading from Great Nash [Grid Ref. SM/9750 0949], mapped as Rosemarket Beds (Strahan *et al.*, 1914 : 112), in fact yields an Ashgill fauna.

Thus there are two nominal species of *Ygerodiscus* (having eliminated *maccoyi* and *compressa*) viz. *undulatus*, from the late Rhuddanian or Idwian of Meifod, and *plicatus* from the Idwian or early Fronian of Pembrokeshire. There is an age gap of between nought and about seven million years depending on the correlation chosen, and a geographical separation of a hundred miles. Half way between these localities, at Llandovery itself, occur several populations of *Ygerodiscus* which can be unequivocally dated as being Idwian in age (see localities above). These populations confirm the view that the two forms are so close that any separation would be invidious. Thus *plicatus* is treated here as a junior synonym of *undulatus*.

The species is just as denticulate as *Eoplectodonta*. Jones (1928 : 456) suspected the presence of denticles in *undulatus*, and illustrated them in *plicatus* and *compressus*, but neither Kozlowski (1929) nor Williams (1951) referred the species to *Plectodonta* ; Havlíček (1967) referred all four names to *Ygerodiscus*.

As discussed earlier under the genus, *Ygerodiscus undulatus* probably evolved from end members of *Eoplectodonta duplicata* populations at some time during the late Rhuddanian. That the two became genetically distinct quite quickly is indicated by the presence in the collection from Meifod of numerous smallish *Y. undulatus* intimately associated with a few larger *E. duplicata*, without forms connecting the two groups.

? *Ygerodiscus cornutus* (Davidson)

(Plate 13, figs. 11, 12, Plate 14, figs. 1, 2)

1883 *Leptaena segmentum* var. *cornuta* Davidson : 166, pl. 12, figs. 1–3.
1928 *Sowerbyella cornuta* (Davidson) Jones : 461.
1967 *Ygerodiscus cornutus* (Davidson) Havlíček : 62.

MATERIAL. Four specimens in the Davidson Collection, from Middle Wenlock Shales (Coalbrookdale Beds), half a mile west of Buildwas Abbey, Shropshire.

England, all registered B 5828. A lectotype is selected here (Plate 13, figs. 11, 12), and has been re-registered BB 32416.

MEASUREMENTS (in mm.)

	l.	w.
BB 32416, conjoined valves, lectotype	5·4	11·2
B 5828, conjoined valves	4·5	8·9

DISCUSSION. All four specimens consist of conjoined valves, and their internal details are largely unknown. However, when viewed through water, denticles are visible along the hinge line, and the species is tentatively referred to *Ygerodiscus*, as suggested by Havlíček (1967), since the valves are to some extent undulate. It is however possible that it should belong in *Eoplectodonta*, but the species is distinct from contemporary sowerbyellids in its different outline, which is trapezoidal, with antero-lateral pojections. ?*Ygerodiscus cornutus* is rare ; only four specimens were collected from more than a ton of the shale washings processed by Maw and Davidson, in other respects richly fossiliferous.

Anisopleurella Cooper 1956

1956 *Anisopleurella* Cooper : 804.
1965 *Anisopleurella* Cooper ; Williams : H380.

TYPE SPECIES. *Anisopleurella tricostellata* Cooper 1956.

DISCUSSION. The genus is known by the two Porterfield species originally described by Cooper, *A. tricostellata* and *A. inaequistriata*, and by *A. balclatchiensis* (Reed 1917) from the contemporary Balclatchie Mudstones of Scotland (Williams 1962 : 185). In addition Cooper (1956 : 805) attributed *Orthis quinquecostata* M'Coy 1846 to *Anisopleurella* and Williams (1962 : 187) attributed *Sowerbyella multiseptata* Williams 1955. Havlíček (1967 : 55) described *A. ovalifera* from the Ashgill of Bohemia and also attributed *Sowerbyella gracilis* Jones to the genus without redescription. *A. gracilis* is the only post-Ordovician species yet recorded.

Dr. G. A. Cooper has kindly sent over on exchange topotype specimens of *Anisopleurella tricostellata*, (BB 32855–6) from the Pratt Ferry Formation (basal Caradoc) of Alabama, for comparison with *A. gracilis*.

Anisopleurella gracilis (Jones)

(Plate 16, figs. 1–9)

1914 *Plectambonites* cf. *quinquecostatus* (M'Coy) ; Jones *in* Strahan *et al.* : 80 *et seq.*
1928 *Sowerbyella gracilis* Jones : 472, pl. 24, figs. 21–25.
1967 *Anisopleurella gracilis* (Jones) Havlíček : 55.

DIAGNOSIS. Small *Anisopleurella* with thin shell curved socket plates and petaloid muscle field. Few structures in the pedicle valve.

DESCRIPTION. Owing to the thinness of the shell, the specimens have all suffered crushing, in most cases severe, during the compaction of the fine shale in which they

are found. Thus details of the following description will doubtless be amplified if good uncrushed material, especially with shell preserved, is later found.

Exterior. Brachial valve concave, pedicle valve convex. Outline semicircular and alate. Umbo usually incurved, and hinge line enrolled. Small node at the otherwise concave umbo of the brachial valve. Maximum width at hinge line. Ornament unequally parvicostellate, with three (Plate 16, fig. 7) or more larger ribs and large number of small parvicostellae between them. In some shells, particularly those with many primary ribs (as many as 20) the distinction between the strength of the two types of ribs breaks down, and there are more or less equally parvicostellate areas. Growth lines not usually seen. Small undulations sometimes present. Faint small rugae occasionally laterally. Interarea difficult to see clearly on account of crushing, delthyrium possibly open, but a small deltidium or perhaps a pair of small deltidial plates is suspected. Trifid cardinal process visible from exterior ; chilidial structures uncertain. Apical foramen not seen. Very prominent " ribs " seen on many exteriors (Plate 16, figs. 1, 3, 4, 7, 8) due to post-mortem crushing, when the relatively stout brachial valve septa got pushed through the thin shell of both valves.

Pedicle Valve Interior. In a few pedicle valves from the Cartlett Beds there appear to be very faint crenulations on the hinge line ; however they are too faint to be called denticles and are absent from most specimens, whose hinge lines seem quite smooth. No teeth, but weak dental plates, merging with valve floor a short distance anteriorly. No median septum ; no muscle bounding ridges. No trace of the muscle field or vascular markings. Shell often covered with papillae outside the smooth central area, but papillae size small.

Brachial Valve Interior. Clavicular plates very thin, diverging widely, curving right round parallel to, and trending posteriorly towards, the hinge line. Cardinal process small for a plectambonitacean. Median septum approximately half-way to anterior margin. Inner side septa thin, running anteriorly to about the same distance as the median septum. Outer side septa strong, starting posteriorly only just anterior of the cardinal process, becoming wider anteriorly, but usually not as far as inner side septa. Bema curving round anteriorly from beneath clavicular plates, with valve floor antero-laterally of outer side septa, giving a bi-petaloid central field. Muscle system and vascular system not seen. Small papillae common outside central field.

Type specimen. Holotype (by original designation of Jones 1928, caption to Plate 24, fig. 21) GSM 37554, an external mould of a pedicle valve from the Cartlett Beds, south side of railway cutting, 650 yards SW of Priory Mill, SE of Haverfordwest, Pembrokeshire, Wales.

Dimensions (in mm.)

	l.	w.
GSM 37554, mould of both valves, holotype (Plate 16, fig. 1)	5·0	approx. 9
GSM 37551, external mould of pedicle valve (Pl. 16, figs. 4, 7)	4·2	7·9

	l.	w.
BB 32043, external mould of brachial valve	5·1	9·5
BB 32028, external mould of brachial valve	2·6	approx. 4
BB 31996, external mould of brachial valve	3·9	7·2
BB 32049, external mould of brachial valve	5·0	8·5

Discussion. This small species occurs commonly at only one general locality and horizon, near the base of the Silurian in Pembrokeshire. The actual type locality is now obscured by grass on the cutting, but a good collection (BB 31995–32054) was obtained in 1968 about 20 yards west of the type locality [Grid Ref. SM/9564 1458] from a patch cleared for a new telegraph pole : the specimens seem indistinguishable from those in the type collection (GSM OTJ 766–90).

Anisopleurella gracilis also occurs rarely in the upper part of the Rhuddanian at Meifod (Temple 1970, in press). Jones (1928 : 473) and Williams (1951 : 130) record the species from as high as C_1 in the Llandovery area, but the present author has not seen material from above the Lower Llandovery.

Subfamily **AEGIROMENINAE** Havlíček

Havlíček (1967) included the following genera within the Aegiromeninae :—

Aegiria Öpik 1933
Aegiromena Havlíček 1961
Aegironetes Havlíček 1967
Chonetoidea Jones 1928
Sentolunia Havlíček 1967
Sericoidea Lindström 1953

Havlíček noted two main differences between the two subfamilies of the Sowerbyellidae, firstly the Aegiromeninae have a " circular or cordate visceral field ", whilst in the Sowerbyellinae the field is " halved into two oval lobes ". Secondly, in the Sowerbyellinae " in the longitudinal axis of each of the two lobes, there is a septum which evidently served for the attachment of adductors. In Aegiromeninae, however, adductors were directly attached to the bottom of brachial valve " (1967 : 37–8).

Apart from rare specimens of *Aegiromena* itself, the only two of these genera recorded from the Silurian are *Aegiria* and *Chonetoidea*, which are reviewed below. Since *Chonetoidea* has been so widely quoted, the opportunity is taken to describe and figure the type species, *C. papillosa*, from the Ashgill of Pembrokeshire ; Reed's original description has remained unamended.

Aegiromena Havlíček 1961

? ***Aegiromena*** sp.

(Plate 16, figs. 13, 14)

Discussion. A single pedicle valve, from the Middle Llandovery, Idwian, of Newlands, in the Craighead Inlier, near Girvan, Ayrshire, Scotland, may be tenta-

tively referred to this genus. Havlíček (1967) has described several species of *Aegiromena* from the Bohemian Ordovician, including *A. ultima* from the Upper Ashgill (Marek & Havlíček 1967), and in addition a single species, *A. myrmido* (Barrande) from the Litěn Formation, of Wenlock age. The genus has never been recorded from the Llandovery (apart from Temple's record (1968) of " *Aegiromena* sp. nov. " from the very base of the Llandovery).

The internal mould of the pedicle valve is typical of the genus, but the corresponding external mould shows an unequally parvicostellate ornament with occasional strong, widely spaced costae similar to those seen on *Leangella scissa*. Thus the final attribution to *Aegiromena* seems best left with a query, as the ornament of plectambonitaceans is capable of a very high degree of variation.

MEASUREMENTS (in mm.)

	l.	w.
HML 9931 Internal mould of pedicle valve (Plate 16, figs. 13, 14)	3·5	approx. 7

Chonetoidea Jones 1928

1928 *Chonetoidea* Jones : 389.
1933 *Chonetoidea* Jones ; Öpik : 51.
1957 *Chonetoidea* Jones; Spjeldnaes : 104.
? 1960 *Chonetoidea* Jones ; Sokolskaya : 210.
1965 *Chonetoidea* Jones ; Williams : H383.
1967 *Chonetoidea* Jones ; Havlíček : 48.

Chonetoidea (type species *C. papillosa* (Reed 1905) from the Ashgill of Pembrokeshire) was erected by Jones in 1928 to cover all of what he knew of the subfamily. Five years later Öpik (1933) erected *Aegiria* (type species *A. norvegica* from the Llandovery of the Oslo region), and detailed the following differences between the two genera in the form of a table (1933 : 51), comparing *papillosa* and *garthensis*, referring the latter species to *Aegiria*. His table has been kindly translated by Dr. R. P. S. Jefferies as follows :—

papillosa (Jones 1928, pl. 25 fig. 21 and Reed 1905, pl. 23, fig. 13)	*garthensis* (Jones 1928, pl. 25, fig. 26)
Brachial lamellae scarcely indicated	Brachial lamellae strongly developed and sharply defined
Cardinal pit deep with clear borders	Cardinal pit scarcely indicated
Median septum weak, side septa present	Median septum large ; no trace of side septa

In fact both species show comparable brachial lamellae (termed the bema in this paper), although they are stronger in *garthensis*. The cardinal pit (i.e. the hollow area immediately anterior of the cardinal process) is, if anything, deeper in the second specimen of *garthensis* (GSM 50417–8) than in any specimen of *papillosa* ; unfortunately the illustrated holotype of *garthensis* is slightly damaged near the cardinal pit, so although Öpik's observation was justified on Jones' illustration, his statement is incorrect.

However Öpik's third point, on the distribution of structures within the brachial valve, is certainly important. *Chonetoidea papillosa* has a number of structures (Plate 17, fig. 1), some of which are no more than elongated papillae, whereas all the species of *Aegiria* have a pronounced median septum and very little trace of side septa, and this appears to be a character of generic difference. The indefinite structure of *C. papillosa* is shared by *C. iduna* Öpik 1933 and *C. virginica* Cooper 1956, though the latter species, and also *C. gamma* Spjeldnaes 1957, both have differentiated ornament, and are probably referable to *Sericoidea* (this was suggested for *virginica* by Williams 1962 : 189). On the other hand, Spjeldnaes (1957 : 105, fig. 24) illustrates another two species, *C. alpha* and *C. stoermeri*, as possessing well-defined median septa, as well as many small side septa round a bema. *C. stoermeri* is one of the earliest members of the group, coming from Zone 4a and 3, equivalent to Llandeilo in age. However *C. alpha* and *C. stoermeri* might perhaps be placed in *Aegiromena* ; but revision of Ordovician forms is out of place in the present work, sufficient to say that *Chonetoidea* and *Aegiria* will be kept distinct until a detailed analysis of Ordovician forms is available.

As far as is at present known, despite many records to the contrary, *Chonetoidea* does not occur in the Silurian.

The form illustrated as " *Chonetoidea simorini* M. Borrisiak in coll. " from the Middle Ordovician of Kazakhstan by Sokolskaya (1960, pl. 27, figs. 24, 25) does not look as though it ought to belong in *Chonetoidea*.

Chonetoidea papillosa (Reed)

(Plate 17, figs. 1–3)

1905 *Plectambonites papillosa* Reed : 451, pl. 23, figs. 13–15.
1914 *Plectambonites papillosus* Reed, Jones *in* Strahan *et al.* : 67.
1928 *Chonetoidea papillosa* (Reed) Jones : 498, pl. 25, figs. 20–24.
1965 *Chonetoidea papillosa* (Reed) ; Williams : H383, fig. 244, 3a–c.

Diagnosis. *Chonetoidea* with a large number of subequally parvicostellate ribs. Small thin median septum in brachial valve, with large number of small side septa surrounding a faint bema.

Description. *Exterior.* Pedicle valve convex, brachial valve concave. Lateral profile gently curved, without enrollment of hinge line or umbo. Outline semicircular, only slightly alate. Size small for the family (maximum width 7 mm. in the type sample of 20 specimens). Ornament of large number of more or less equal parvicostellae (Plate 17, fig. 3) ; apparently random ribs sometimes stand out as stronger, but there seems to be no pattern in their distribution. Undulations (except tectonic), rugae and growth lines absent. Interarea wide, with both valves in nearly the same plane. Small arched deltidium. Trifid cardinal process clearly visible ; no chilidial plates or chilidium. Small but prominent protegular node on brachial valve. Foramen very small not usually seen, but there is evidence from several pedicle internal moulds (SMA 30848 etc.) that it was probably functional.

Pedicle Valve Interior. Hinge line finely denticulate (best seen on SMA 30847 and

SMA 11313). Along inside of hingeline, appearing as nodes on internal moulds, there are also small pits, up to two on each side of the umbo, not present in all specimens. Small pair of teeth and dental supports, too slight to be termed dental plates, on each side of the pedicle chamber. Faint and short median septum immediately anterior of pedicle area. Muscle scars and vascular system too faint for detailed description. Papillae near alae and anterior margin, finer than in brachial valve. Shell very thin, allowing exterior ornament to be seen on valve interior.

Brachial Valve Interior. Fossettes, although presumably present to accommodate pedicle valve denticles, not seen with certainty. Strong socket plates whose angle of divergence varies from 80 to 130 degrees, sometimes straight, sometimes curving round towards hinge line. In one specimen (SMA 11313) they split into two near their antero-lateral extremities. Between socket plates, anterior cardinal process, a hollow extending nearly to valve exterior. Thin median septum and many approximately equal-sized side septa, which may or may not be symmetrical. Faint bema in some specimens, absent in others. Sometimes small side septa cut through bema edge. Muscle field indistinct ; vascular system not seen. Papillae often quite large, grading into the small side septa.

Type specimen. Lectotype (here chosen) SMA 11311 (Plate 17, fig. 1), the original of Reed 1905, pl. 23, fig. 13. V. M. Turnbull Collection. Slade Beds (Ashgill), Upper Slade, Haverfordwest, Pembrokeshire, Wales.

Dimensions (in mm.)
All specimens from the type locality.

		w
SMA 11311 Brachial internal mould, lectotype (Plate 17 fig. 1)	2·5	5·9
SMA 30841 Pedicle external mould, (Plate 17, fig. 3)	3·1	5·3
SMA 30848 Conjoined valves	3·4	5·9
SMA 30844 Pedicle external mould	1·7	3·4
SMA 30845 Conjoined valves	3·2	4·8

Discussion. Havlíček (1967 : 49) described very small canals penetrating the pedicle valve interarea in *Chonetoidea radiatula* (Barrande) from the Ashgill Králův Dvůr shales of Bohemia. He notes that the fillings of these canals are only " exceptionally " preserved, and that on most of his specimens they are represented only by fine nodes on the interior of the mould of the pedicle valve. *Chonetoidea papillosa* also shows these nodes, although in no case in the type collection are any canals themselves preserved. The very fine denticulation on the hinge line, seen only on the larger specimens, has not previously been noted. Since they are contemporary, and do not appear to differ greatly from each other in material detail, it is possible that *C. papillosa, C. radiatula* and *C. tenerrima* Havlíček 1952 might in future be synonomised ; certainly the latter two species do not appear distinct, and occur in the same formation.

Aegiria Öpik 1933

1933 *Aegiria* Öpik : 55.
1952 *Aegiria* Öpik ; Havlíček : 399 etc *pars.*
1965 *Aegiria* Öpik ; Williams : H381.
1967 *Aegiria* Öpik ; Havlíček : 38.

TYPE SPECIES. *Aegiria norvegica* Öpik 1933, from the Middle Llandovery (Zone 6c) of Leangen, near Oslo, Norway.

DISCUSSION. The relationships between *Chonetoidea* and *Aegiria* are discussed above. The line between the two genera (and *Sericoidea* with its unequal parvicostellae) is finely drawn when the complete range of variation is taken into account ; however Öpik's separation of the two genera is endorsed here.

So far as is known, *Aegiria* does not occur in the Ordovician. During the Silurian its occurrence is patchy ; in parts of the Llandovery and Ludlow it is present in swarms, in the Wenlock it is rare.

Silurian species assigned to *Aegiria* are as follows :—

Chonetoidea garthensis Jones 1928 : 500, pl. 25, figs. 25, 26, from the Lower Llandovery of Wales.

Leptaena grayi Davidson 1849 : 271, figs. 1, 1a, from the Wenlock Limestone of Dudley, England.

Aegiria norvegica Öpik 1933 : 55, pl. 10, figs. 1–5, pl. 11, figs. 3–5, from the Middle Llandovery of Leangen, near Oslo, Norway.

Chonetoidea sp. Borrissiak 1955 ; 50, pl. 9, figs. 9–13 from the Llandovery of the Chinghiz mountains of Kazakhstan, U.S.S.R.

Aegiria thomasi Talent 1965 : 24, pl. 6, figs. 1, 3, 5-7 from the Dargile Formation (Ludlow) of the Heathcote District, Victoria, Australia.

The following species may be referable to *Aegiria*, but require further investigation:

Plectambonites aequalis Teichert 1928 : 58, pl. 5, figs. 18–20, from the Middle to Upper Llandovery of Kiltsi, Estonia, U.S.S.R.

Plectodonta aknistensis Rybnikova 1967 : 188, pl. 19, figs. 1, 2, from Late Wenlock and Early Ludlow boreholes in Latvia, U.S.S.R.

Sowerbyella austrum Öpik 1953: 14, pl. 3, figs. 17, 18 from the Illaenus Band of the Wapentake Formation (Upper Llandovery), Heathcote District, Victoria, Australia.

Aegiria garthensis (Jones)

(Plate 17, figs. 4–7)

1928 *Chonetoidea garthensis* Jones : 500, pl. 25 figs. 25, 26.
1933 *Aegiria garthensis* (Jones) Öpik : 51 etc.

DIAGNOSIS. Large *Aegiria* with many ribs, well-defined bema, and very divergent strong socket plates.

DESCRIPTION. The specimens originally described by Jones are still the only ones available, these are part and counterpart of two brachial valves, and thus the following description of the exterior is based only upon the brachial valve.

Exterior. Shape of brachial valve gently concave, with very slight median sulcus. Outline semicircular, and slightly alate. The two specimens known are rather large for the genus. Ornament of subequal parvicostellae (about 65 in number) of greater size in the central part of the valve than towards the ears. New ribs arise by intercalation and division. No rugae, undulations or growth lines are visible, but the parvicostellae are wavy and irregular in places in an apparently random fashion. Interarea fairly narrow, no chilidium or chilidial plates. Cardinal process visible from exterior, growing out posteriorly from hinge line. Small, poorly defined protegular node present.

Pedicle Valve Interior. Unknown.

Brachial Valve Interior. Hinge line apparently smooth. Strong pair of divergent socket plates, curving round to end up almost parallel with hinge line. Cardinal process and socket plates form posterior wall of small pit extending nearly to valve exterior. Immediately anterior of this there is the median septum, prominent and situated on top of the fold, so that all the anterior part of the valve interior appears divided into two parts. Bema is well defined ; no side septa. No muscle scars or vascular system seen. Exterior ornament seen on interior (outside the bema), but modified by papillae, which are slightly elongated and arranged in rows upon some of the exterior troughs providing an irregular pattern.

Type specimens. Holotype GSM 37589–90, a brachial valve (the part and counterpart are registered under two separate numbers), designated by Jones 1928, caption to pl. 25. Jones gives the locality as " Lower Llandovery (middle part) ; N. of Garth, Breconshire ". G. Andrew Collection.

Dimensions (in mm.)	l	w
GSM 37589–90, brachial valve, holotype (Pl. 17, figs. 5, 6)	2·8	approx. 8
GSM 50417–8, brachial valve (Pl. 17, figs. 4, 7)	3·4	8·8

Discussion. The locality given by Jones for the species is vague, and the species name was not used in the stratigraphical description of the Garth area (Andrew 1925) because it predates Jones's work. Jones' description is unhelpful since all the Llandovery of the Garth area is north of the village of Garth and the middle part of the Lower Llandovery (presumably Andrew's division Ab) has the largest outcrop of any division in the area. One of the specimens has λ 4 on it, but this cannot be correlated with Andrew's published localities since his locality 4 is in the Upper Bala. The only plectambonitids which Andrew cites from his division A b (1925 : 396) are *Plectambonites undulatus* and " a single specimen of *Plectambonites duplicatus* ", so that the locality of the type specimens of *Aegiria garthensis* must remain doubtful. Some collecting by the present author in the Garth area has not produced further material.

Öpik (1933 : 55, pl. 10 figs. 1–5, pl. 11, figs. 3–5) in his excellent description of *Aegiria norvegica*, compares it with *garthensis*, but many of his points of difference are debateable, and it is quite possible that the two species are synonymous. However, without knowledge of the pedicle valve of *garthensis* it would be premature to place *norvegica* into its synonymy.

Aegiria grayi (Davidson)
(Plate 17, figs. 8–14)

1849 *Leptaena grayi* Davidson : 271, figs. 1, 1a.
1852 *Leptaena* ? *minima* J. de C. Sowerby ; M'Coy : 235.
1871 *Chonetes* ? *minima* (J. de C. Sowerby) Davidson : 334, *pars*, pl. 49, figs. 16, 19, ? figs. 17, 18, *non* fig. 15.
1928 ? *Chonetoidea grayi* (Davidson) Jones : 500.
1928 *Chonetoidea* ? sp. 2 Jones : 502.
1963 *Chonetoidea grayi* (Davidson) ; Holland, Lawson & Walmsley : pl. 5, fig. 2.
1968 *Aegiria grayi* (Davidson) Cocks : pl. 12, fig. 3.

DIAGNOSIS. *Aegiria* with relatively few ribs, which are angular at their crests and troughs. Bema poorly defined. Coarse brachial valve papillae are mainly subcircular rather than elongate.

DESCRIPTION. *Exterior.* Pedicle valve gently convex, brachial valve flat to slightly concave, both valves with slight median fold and sulcus. Outline semicircular, with only an hint of alation. Size is small for genus (maximum width less than 5 mm. in topotype collection of 35 specimens). Usually between 20 and 30 ribs, no specimen seen with more than 40, but counting is difficult near the alae, since the ribs are much finer there. Ribs more angular in cross section than *A. garthensis*. No rugae or undulations seen. Growth lines occasionally visible near anterior margin. Interarea relatively large, the two valves making shallow angles with each other. Small deltidium; no childidium or chilidial plates. Cardinal process clearly visible from valve exterior. Small but distinct apical foramen, probably functional, and protegular node at apex of brachial valve, forming base to cardinal process.

Pedicle Valve Interior. No evidence of hinge line denticulation. Teeth supported by dental plates which flare antero-laterally, merging slowly with valve floor as bounding ridges to posterolateral part of muscle field. Pedicle chamber bounded posteriorly by deltidium and laterally by teeth and dental plates. Some secondary calcite immediately anterior of pedicle opening, which falls away anteriorly before being raised again to form slight swell of the rather faint and short medium septum. Diductor scars lanceolate on either side of median septum between large adductor scars, at 60 to 90 degrees to each other. No vascular markings seen. Exterior ornament conspicuous from interior. Some papillae outside central muscle field, but much finer than in brachial valve.

Brachial Valve Interior. No fossettes seen on hinge line. Strong socket plates. Anterior to cardinal process a pit extends nearly to valve exterior at protegular node, anterior of which is strong median septum extending three quarters of the way to anterior margin. Small trace of side septa. Bema visible, but usually only faintly developed. Outside this several coarse papillae relatively amongst the largest of any strophomenide. These papillae subcircular, rather than elongate as *A. garthensis*. In Upper Llandovery (Plate 17, fig. 12) papillae pattern seems random, by Ludlow time, however, they are roughly arranged into two or more concentric rings (Plate 17, fig. 14). Faint radial striae sometimes seen on surface of bema, possibly reflection of exterior ornament or striations upon muscle field similar to *Leangella*. Vascular system not seen.

LECTOTYPE (here chosen) B 780, (Plate 17, fig. 9), a pair of conjoined valves from the Wenlock Limestone of Dudley, Worcestershire, England. John Gray collection, presented to the Museum in 1869. Davidson (1849 : 271) based his descriptions on specimens found by Gray and Fletcher at Dudley, and there is no material in the Davidson Collection.

LOCALITIES AND MATERIAL. Wenlock Limestone (Upper Wenlock), " Dudley ", Staffordshire, England. Gray and Caroline Birley Collections, no exact locality. (Plate 17, figs. 9, 10) (B 780, B 23205 etc.).

Hughley Shales (Llandovery, Telychian), stream bank at Domas, near Harley, Shropshire, England. Grid Ref. SJ/5936 0062. (Plate 17, fig. 8) (OUM C13403–56).

Hughley Shales (Llandovery, late Fronian or early Telychian), north bank of River Onny, Shropshire, England. Grid Ref. SO/4260 8532. (Plate 17, figs. 11, 12) (OUM C12046–C12155).

Hughley Shales (Llandovery, Telychian), south-west bank of Heath Brook, 500 yards ENE of the Plough Inn, Wall-under-Heywood, Shropshire, England. Grid Ref. SO/5120 9276. (OUM C13056–75).

C_3 Beds (Llandovery, Fronian) roadside outcrop on Cefn Cerig road, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7751 3257. (BB 32116–35).

Chonetoidea grayi Beds (Ludlow, upper Leintwardinian), Pont Shoni, near Builth Wells, Radnorshire, Wales. Grid Ref. SO/078 468. (Plate 17, figs. 13–14). (BB 32430–1 etc.).

DIMENSIONS (in mm.)	l	w
B 780 conjoined valves lectotype (Plate 17, fig. 9), Dudley.	2·7	4·3
B 23205 conjoined valves (upper central specimen in Pl. 17, fig. 10) Dudley.	2·7	4·1
OUM C13974 conjoined valves (central specimen in Pl. 17, fig. 8) Hughley.	1·8	3·0
OUM C13425 (1st specimen) conjoined valves Domas.	1·9	2·9
OUM C13425 (2nd specimen) conjoined valves Domas.	1·4	2·3

DISCUSSION. The description is based on the topotype collection for the exterior, and on a collection from the Hughley Shales (Upper Llandovery) of the Onny River for the interior.

" *Chonetoidea* " *grayi* has been widely quoted in recent years from various horizons in the Silurian, chiefly from the British Ludlow ; indeed Chonetoidea grayi Beds is used as a rock formation name in the Builth district (Straw 1937).

The late Professor W. F. Whittard had already selected the lectotype, but he was kind enough to hand over his notes on the species to the present author. At the time of his original description, Davidson was not familiar with *Leptaena minima* J. de C. Sowerby 1839, but in his monograph (1871 : 335) he put *grayi* into the synonymy of *minima*, although not without doubts. An examination of the holotype of *minima* (GSM Geol. Soc. Coll. 6639) reveals different ribbing from *grayi* and also a spine base on the hinge line, indicating that *minima* is a chonetid, perhaps referable to *Protochonetes* Muir Wood 1962.

As may be seen from Plate 17, *Aegiria grayi* differs from the Lower Llandovery *A. garthensis* (and also *A. norvegica*) in its fewer and more angular ribs, and its less well defined bema. The form of *A. grayi* differs from the Upper Llandovery (Plate 17, figs. 11, 12) to the Ludlow (Plate 17, figs. 13, 14) and a study of the species group is intended by the present writer.

VII. ACKNOWLEDGMENTS

I am most grateful for valuable discussion with many people, in particular Dr. M. G. Bassett, Dr. M. J. S. Rudwick, Dr. J. T. Temple and Professor A. Williams. I also thank Dr. G. F. Elliott for a constructive reading of the manuscript. Dr. V. Havlíček and Dr. J. Bergström have kindly led me to localities in Bohemia and Gotland respectively.

I am obliged to the various authorities at museums ; Mr. J. M. Edmonds and Mr. H. P. Powell of the Oxford University Museum (OUM), Dr. A. W. A. Rushton, Mr. D. E. White, and Dr. P. T. Warren of the Geological Survey (GSM), Mr. A. G. Brighton and Dr. R. B. Rickards of the Sedgwick Museum, Cambridge (SM), Dr. J. K. Ingham of the Hunterian Museum Glasgow (HML), Dr. I. Strachan of the Geology Department, Birmingham University (BU), and Dr. V. Jaanusson of the Naturhistoriska Riksmuseet, Stockholm (RMS). Most of the material is in the British Museum (Natural History) (B and BB). In addition, Dr. A. Martinsson kindly searched in the Wahlenberg collection at Uppsala on my behalf, and Dr. G. A. Cooper sent some choice American specimens on exchange.

I have had valuable technical assistance from Miss L. M. Stokes. The photographs were taken by Messrs P. Green, C. Keates and T. Parmenter, as well as by myself ; Mr. Green also drew Text-figs. 1 and 2.

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PLATE 1

Merciella vesper Lamont and Gilbert

Llandovery, Telychian, Wych Beds, Coneygore Coppice, Worcestershire, England. Lamont & Gilbert Collection.

FIGS. 1, 2. BU 369. Latex cast and internal mould of brachial valve. Figured Lamont & Gilbert 1945 pl. 4, figs. 10, 12. Lectotype, × 4.0.

FIGS. 3, 4. BU 370. Latex cast and internal mould of brachial valve. Figured Lamont & Gilbert 1945 pl. 4, fig. 11. Fig. 3, × 4.0., Fig. 4, × 3.0.

FIG. 5. BU 367. Internal mould of pedicle valve. Figured Lamont & Gilbert 1945, pl. 4, fig. 8. × 4.0.

Leptellininid gen, et sp. indet.

Llandovery, Rhuddanian, Woodland Formation, Woodland Point, near Girvan, Ayrshire, Scotland. Grid Ref. NX/168 952. Mrs. R. Gray Collection.

FIGS. 6, 7. BB 31832. Latex cast and internal mould of brachial valve. Fig. 6 × 4.0, Fig. 7 × 2.1.

FIG. 8. BB 31831. Internal mould of pedicle valve. × 2.1.

Diambonia discuneata (Lamont)

Ashgill, Lower Drummuck Group, east brow of Quarrel Hill, near Girvan, Ayrshire, Scotland. Dr. A. Lamont Collection.

FIG. 9. HML 1983. Internal mould of pedicle valve. Figured Lamont 1935 pl. 7, figs. 18, 19. × 9.0.

FIG. 10. HML 1984. Internal mould of pedicle valve. × 9.0.

Leangella scissa (Davidson)

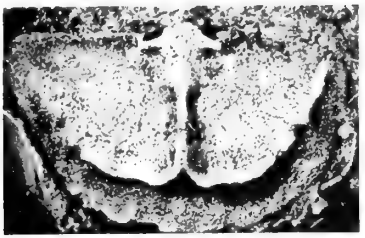
Llandovery, Rhuddanian, Gasworks Mudstone, opposite entrance to the gasworks, Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9558 1533. Author's collection.

FIG. 11. BB 31824. Internal mould of pedicle valve. × 2.0.

FIG. 12. BB 31828. Internal mould of pedicle valve. × 3.0.

FIG. 13. BB 31827. Internal mould of brachial valve. × 3.0.

FIG. 14. BB 31829. Internal mould of brachial valve. × 3.0.



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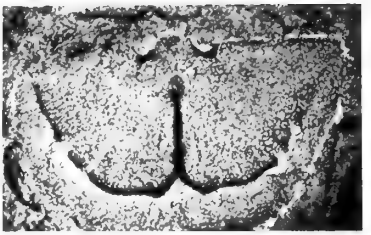

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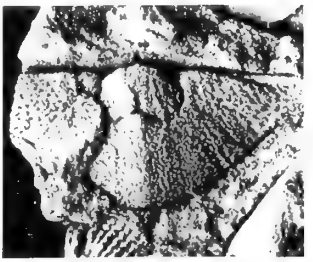

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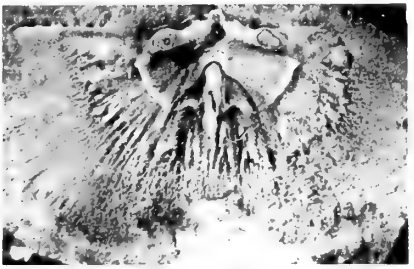

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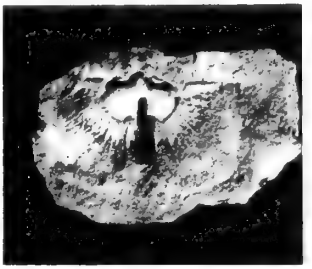

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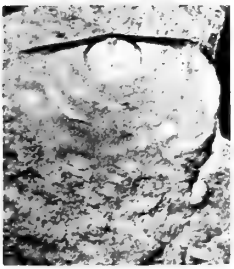

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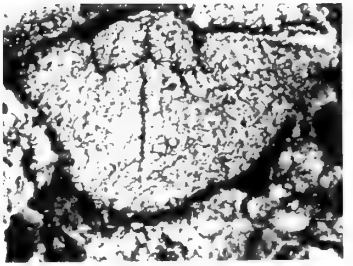

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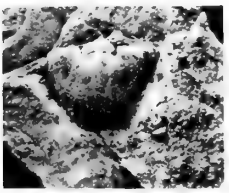

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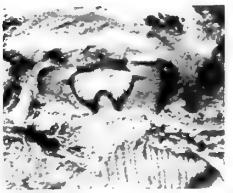

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PLATE 2

Leangella scissa (Davidson)

Llandovery, Rhuddanian, Gasworks Mudstone, opposite entrance to the gasworks, Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9588 1533. Author's collection.

FIGS. 1, 4. BB 32167. Latex casts of the external and internal of a brachial valve. × 5.0.

FIG. 2. BB 31825. Internal mould of pedicle valve. × 3.0.

FIG. 3. BB 31826. Internal mould of brachial valve. × 3.0.

Llandovery, Rhuddanian, Woodland Formation, Woodland Point, Girvan, Ayrshire, Scotland. Grid. Ref. NX/168 952. Mrs. R. Gray collection.

FIG. 5. BB 44620. External view of pedicle valve, figured Reed 1917, pl. 14, fig. 36 (as *Plectambonites segmentum* var. *woodlandensis*, and selected as lectotype of that subspecies in this paper). × 3.0.

FIGS. 6, 7. BB 31836. Two views of an internal mould of a small specimen with conjoined valves. × 8.5.

Llandovery, late Idwian, Venusbank Formation, Hope Quarry, near Minsterley, Shropshire, England. Grid Ref. SJ/3551 0208. Author's collection, except for Fig. 13.

FIG. 8. OUM C9130. Internal mould of pedicle valve. × 4.0.

FIG. 9. OUM C9125. Internal mould of a large pedicle valve, with well impressed vascular system. × 3.0.

FIG. 10. OUM C9127. Internal mould of pedicle valve. × 4.0.

FIG. 11. OUM C9121. Internal mould of brachial valve. × 4.0.

FIG. 12. OUM C9123. Internal mould of pedicle valve. × 4.0.

FIG. 13. B 13673. Internal mould of pedicle valve figured Davidson 1883, pl. 12, fig. 22 (as *Leptaena scissa* Salter). × 6.0.

FIG. 14. OUM C9136. Internal mould of pedicle valve. × 4.0.

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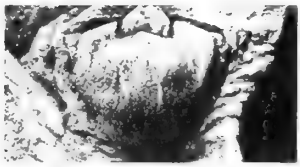

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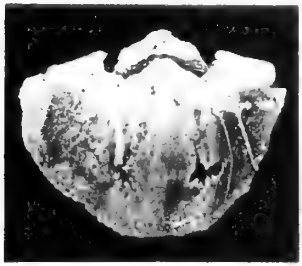

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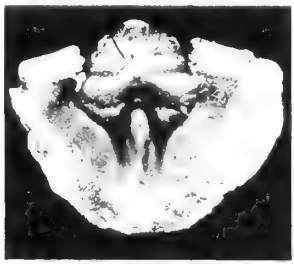

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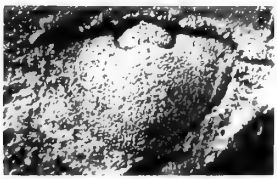

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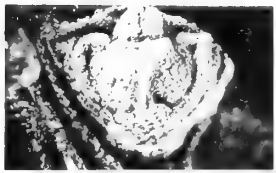

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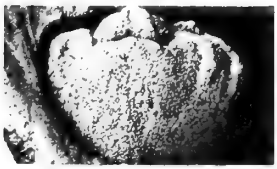

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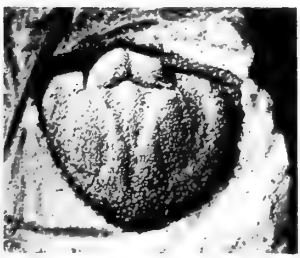

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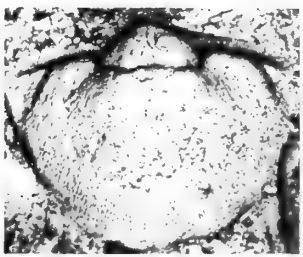

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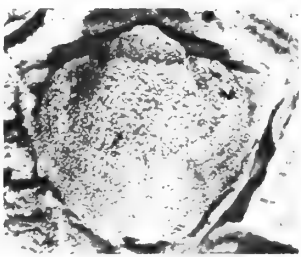

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PLATE 3

Leangella segmentum (Lindström)

Wenlock Limestone (exact locality unknown), Dudley, Staffordshire, England. John Gray Collection.

FIG. 1. B 770. Internal view of a brachial valve. × 5.7.

Leangella scissa (Davidson)

Llandovery, Late Rhuddanian or early Idwian, Newlands Sandstone, near Newlands Farm, Craighead Inlier, near Girvan, Ayrshire, Scotland. Grid Ref. NS/2777 0432. Mrs. R. Gray Collection.

FIGS. 2, 3. B 73644. Internal mould of pedicle valve, from above and behind. × 6.6.

FIG. 4. B 73641. Internal mould of brachial valve. × 5.0.

Llandovery, early Fronian, Venusbank Formation, temporary exposure in field, near Wilmington, Shropshire, England. Grid Ref. SJ/3061 0246. W. F. Whittard Collection.

FIGS. 5, 6. GSM 85286. Latex cast and internal mould of brachial valve. × 2.8.

FIGS. 7–9. GSM 85287. Internal mould and two views of latex cast of a brachial valve. Figs. 7 and 8 × 3.3, Fig. 9 × 7.0.

FIG. 10. GSM 85288. Internal mould of conjoined valves. × 5.1.

Llandovery, early Telychian, C_4 Beds, abandoned quarry on west side of Cefn-Cerig road, near Llandovery, Carmarthenshire, Wales, Grid Ref. SN/7741 3235. Author's collection.

FIG. 11. BB 31675–6. Internal mould of brachial valve. Beneath it is an internal mould of a brachial valve of *Eoplectodonta penkillensis*. × 4.1.

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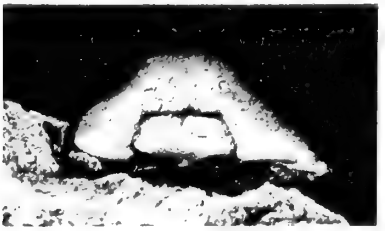

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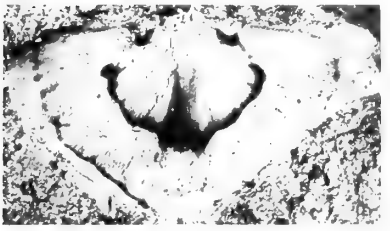

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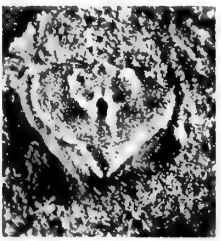

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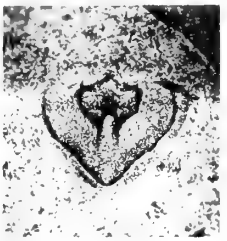

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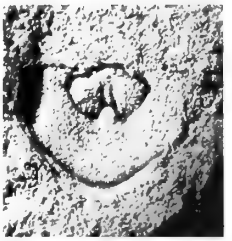

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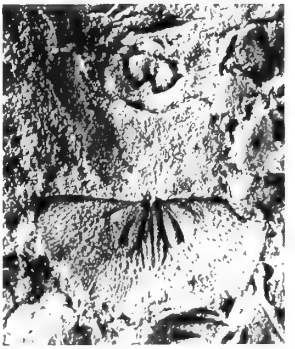

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PLATE 4

Leangella scissa (Davidson)

Llandovery (Fronian). C. Beds, near old footbridge south of Lletty'r-hyddod, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7418 2812. Author's collection.

FIGS. 1, 2. BB 32095. Two views of an internal mould of a pedicle valve. × 6.0.

FIG. 3. BB 32097. Brachial internal mould, × 9.0.

FIG. 4. BB 32103. Pedicle internal mould, × 5.8.

Leangella tufolepta (Havlíček)

Wenlock, Upper Liteň Formation, locality " Hlinik ", near Svaty Jan pod. Skalou, Czechoslovakia. Author's collection.

FIG. 5. BB 32216. Pedicle internal mould, × 5.5.

FIG. 6. BB 32215. Internal mould of conjoined valves, broken off at the subperipheral rim (mounted on a piece of plasticene). × 6.7.

Leangella segmentum (Lindström)

Wenlock, Mulde Marl, Djupvik, Isle of Gotland, Sweden. Angelin Collection, used by Lindström.

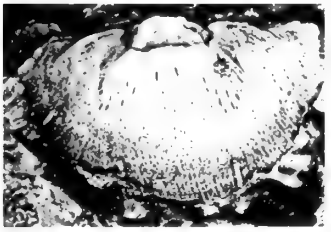
FIGS. 7, 8. RMS Br31602. External views of conjoined valves, × 4.5.

FIG. 9. RMS Br31599. Internal view of brachial valve, × 5.0.

FIG. 10. RMS Br31600. Internal view of brachial valve, × 4.9.

FIG. 11. RMS Br31598. Internal view of brachial valve, lectotype. × 4.6.

FIG. 12. RMS Br31601. Internal view of brachial valve, × 5.7.



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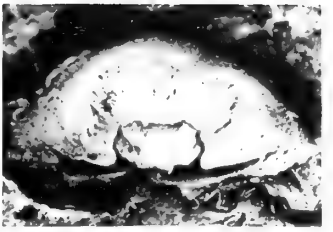

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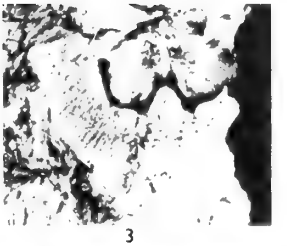

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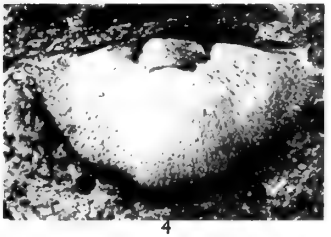

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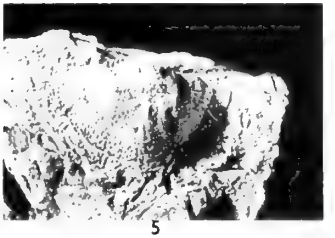

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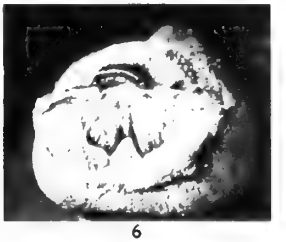

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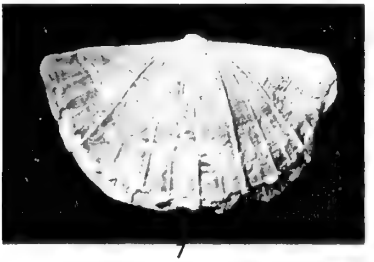

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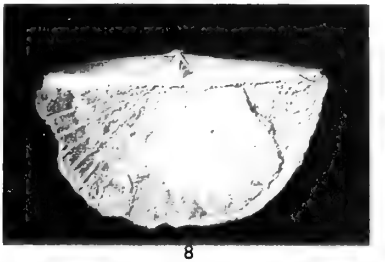

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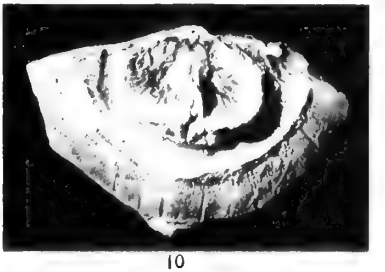

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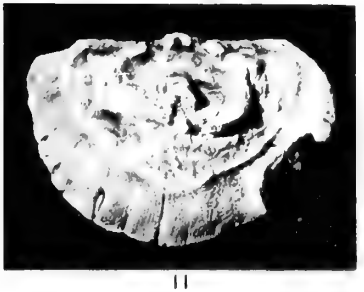

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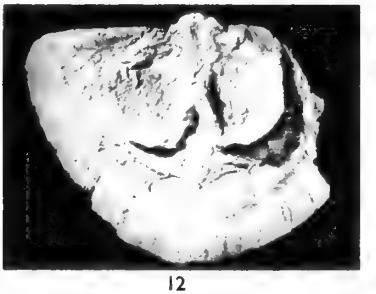

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PLATE 5

Eoplectodonta duplicata (J. de C. Sowerby)

Llandovery, Rhuddanian, " Cefn Rhyddan ", Llandovery, Carmarthenshire, Wales. Sir R. I. Murchison Collection.

FIG. 1. GSM Geol. Soc. Coll. 6877. External mould of brachial valve. Figured J. de C. Sowerby (*in* Murchison) 1839, pl. 19, fig. 2 (as *Leptaena sericea* var.) × 3.2.

FIG. 2. GSM Geol. Soc. Coll. 6874. Internal mould of pedicle valve. Figured J. de C. Sowerby (*in* Murchison) 1839, pl. 22, fig. 2. Holotype. × 3.4.

Llandovery, Rhuddanian, Gasworks Mudstone, opposite entrance to the gasworks, Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9588 1533. Author's collection.

FIGS. 3, 6. BB 31701. Internal mould and latex cast of brachial valve, × 2.0.

FIGS. 4, 7. BB 31699. Internal mould and latex cast of brachial valve. × 2.0.

FIGS. 5, 8. BB 31695. Internal mould and latex cast of brachial valve. × 2.0.

FIGS. 9, 10. BB 31700. Internal mould and latex cast of brachial valve. × 4.0.

FIGS. 11, 12. BB 31696. Internal mould and latex cast of brachial valve. × 4.0.

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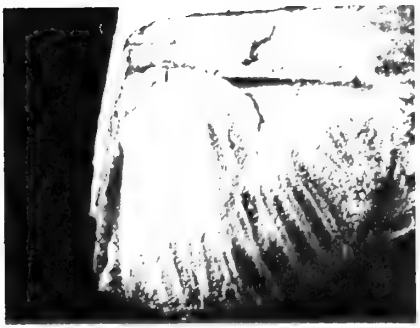

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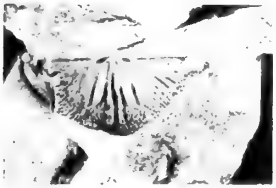

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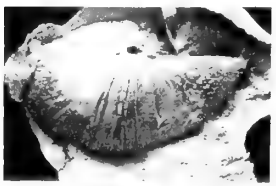

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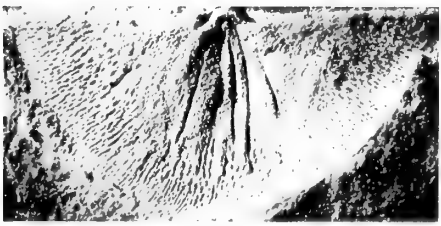

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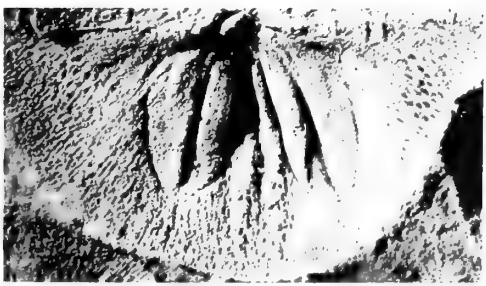

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PLATE 6

Eoplectodonta duplicata (J. de C. Sowerby)

Llandovery, Rhuddanian, Gasworks Mudstone, opposite entrance to the gasworks, Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9588 1533. Collected by C. P. Nuttall and the author.

FIG. 1. BB 31673. Internal mould of pedicle valve with well impressed vascular system. × 3.0.

FIG. 2. BB 31674. Internal mould of pedicle valve. × 3.0.

FIG. 3. BB 31732. Internal mould of pedicle valves. × 1.6.

FIGS. 4–6. BB 31670. Internal mould of brachial valve, and latex cast of it. Fig. 6 is a view of the latex cast from the side, showing the posterior geniculation of the septal field, and its anterior curve, which closely parallelled that of the pedicle valve. Fig. 4 × 3.1., Fig. 5 × 4.2 and Fig. 6 × 2.6.

FIG. 7. BB 31740. Internal mould of pedicle valve. × 1.6.

FIG. 8. BB 31753. Internal mould of pedicle valve. × 1.6.

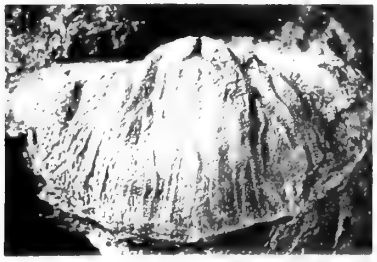
Llandovery, Rhuddanian, Gasworks Mudstone, north end of railway cutting, 150 yards southwest of Haverfordwest Station, Pembrokeshire, Wales. Grid Ref. SM/9588 1563.

FIGS. 9, 14. GSM 37567. Internal mould of pedicle valve, and external mould of brachial valve. The pedicle valve is the holotype of *Sowerbyella precursor* Jones 1928, plate 23, fig. 3 × 2.3. T. C. Cantrill collection.

FIGS. 10, 11. BB 32055. External mould and latex cast of brachial valve, with associated pedicle interarea. × 2.6. Author's collection.

FIG. 12. GSM TCC 1205. Internal mould of brachial valve, × 5.3. T. C. Cantrill collection.

FIG. 13. GSM TCC 1198. Internal mould of pedicle valve, × 3.5. T. C. Cantrill collection.



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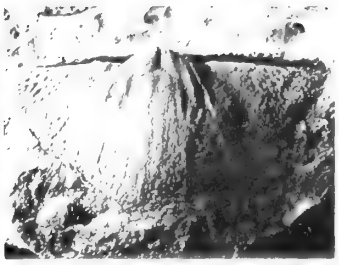

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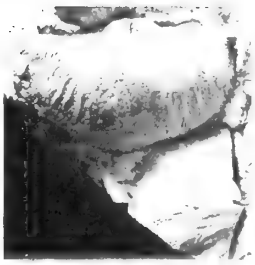

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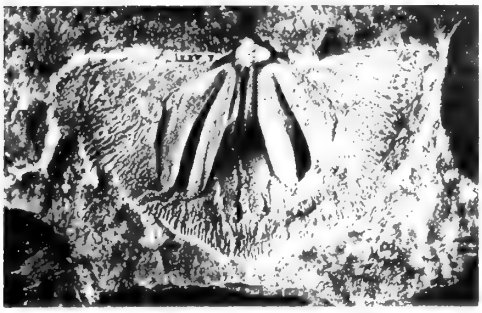

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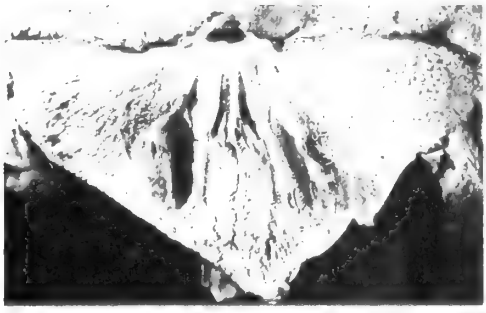

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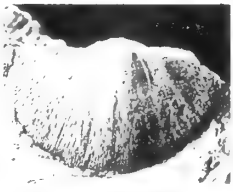

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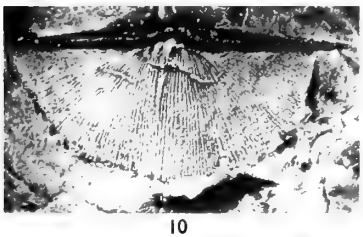

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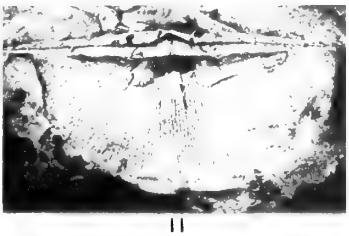

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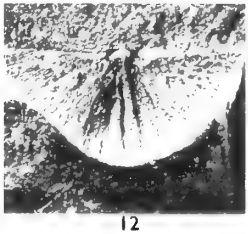

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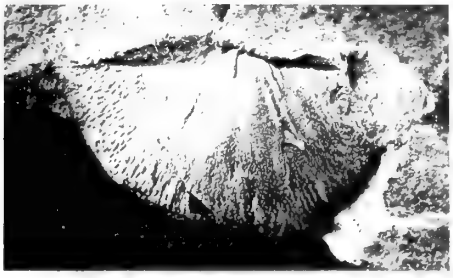

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PLATE 7

Eoplectodonta duplicata (J. de C. Sowerby)

Llandovery, Rhuddanian, Woodland Formation, Woodland Point, Girvan, Ayrshire, Scotland. Grid Ref. NX/168 952. Mrs. R. Gray collection.

FIG. 1. B 44729. External view of pedicle valve. × 2.8.

FIG. 2. B 44734. External view of pedicle valve, × 2.8.

FIG. 3. BB 31830. Internal mould of pedicle valve, with polyzoan colony, × 2.0.

FIGS. 4, 5. BB 31833. Two views of the internal mould of small conjoined valves, × 3.0.

FIGS. 6, 8. BB 31834. Two views of the internal mould of conjoined valves, × 3.0.

FIGS. 7, 9. BB 31835. Two views of the internal mould of conjoined valves, × 3.0.

FIGS. 10, 11. BB 31985. Latex cast and external mould of brachial valve, × 2.5.

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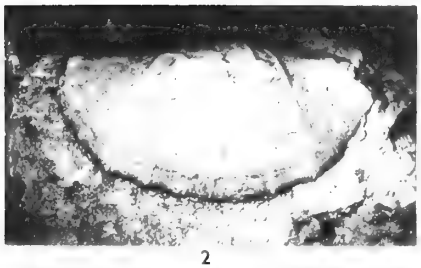

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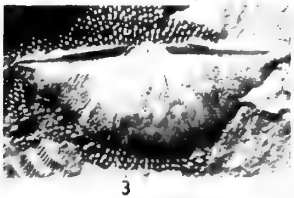

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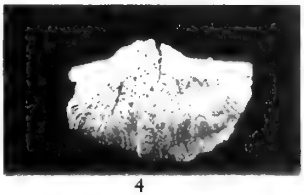

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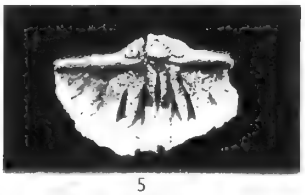

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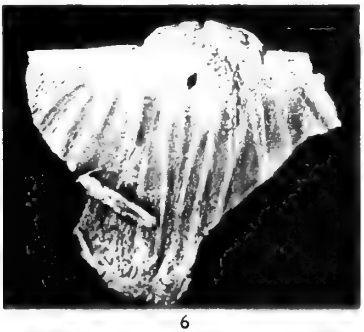

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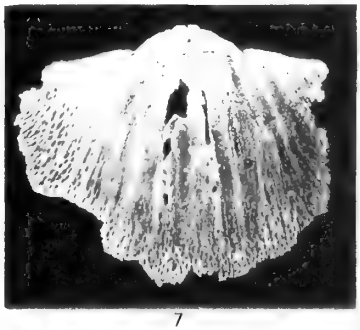

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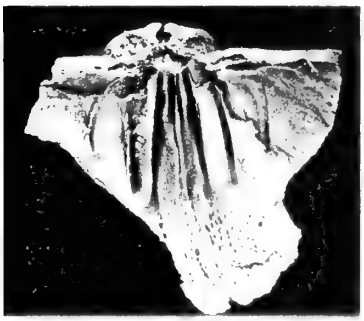

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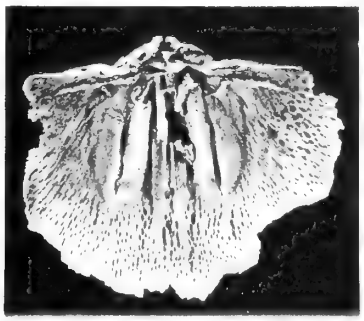

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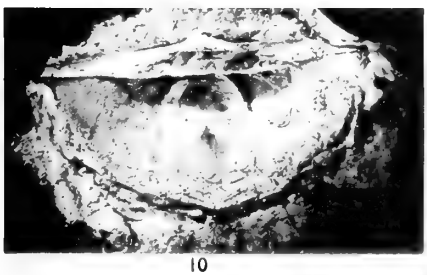

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PLATE 8

Eoplectodonta duplicata (J. de C. Sowerby)

Llandovery, Rhuddanian, Woodland Formation, Woodland Point, Girvan, Ayrshire, Scotland. Grid Ref. NX/168 952. Mrs. R. Gray collection.

FIG. 1. B 73537. External view of pedicle valve, figured Reed 1917, pl. 16, fig. 9 as *Plectambonites transversalis* var. *tricostata*. × 3.7.

FIG. 2. B 73539. External view of pedicle valve, figured Reed 1917, pl. 16, fig. 8 as *Plectambonites transversalis* var. *tricostata*, and selected as lectotype of the subspecies in this paper. × 3.4.

FIGS. 3, 4. BB 31990. Pedicle internal mould and latex cast, × 2.2 and 2.7.

Llandovery, Rhuddanian, Gasworks Sandstone, Union Hill, Haverfordwest, Pembrokeshire, Wales. J. Pringle Collection.

FIGS. 5, 6. GSM 37580. Latex cast and internal mould of brachial valve, figured Jones 1928, pl. 23, fig. 11 as *Sowerbyella superstes*. × 4.8 and 2.5.

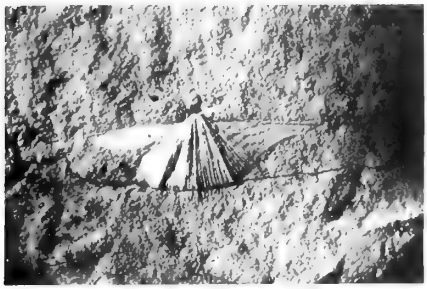
FIGS. 7, 8. GSM 37579. Two pedicle internal moulds on the same slab, fig. 7 is the holotype of *Sowerbyella superstes* Jones, figured Jones 1928, pl. 23, figs. 10, 10a. × 2.9.

Llandovery, Rhuddanian, Mulloch Hill Group, Mulloch Hill, nr. Girvan, Ayrshire, Scotland. Grid Ref. NS/2703 0399. Mrs. R. Gray Collection.

FIG. 9. B 44648. External mould of brachial valve, the counterpart to the specimen figured by Reed 1917, pl. 15, fig. 42 as *Plectambonites transversalis* var. *mullochensis*. × 3.0.

FIG. 10. B 44649. Exterior of pedicle valve, figured Reed 1917, pl. 16, fig. 2 as *Plectambonites transversalis* var. *mullochensis*. × 2.1.

FIG. 11. B 44718. Pedicle internal mould, figured Reed 1917, pl. 15, fig. 41 as *Plectambonites transversalis* var. *mullochensis*, and selected as lectotype of that subspecies in this paper. × 2.5.



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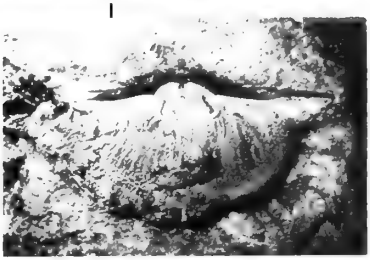

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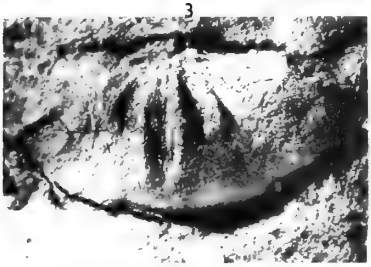

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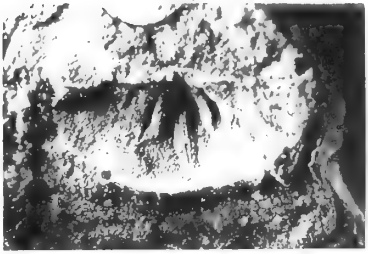

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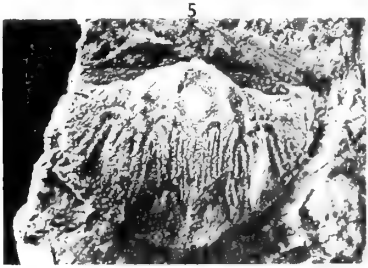

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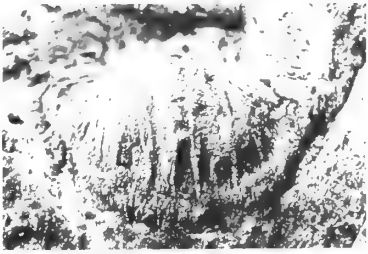

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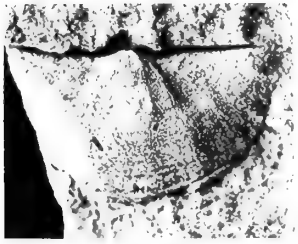

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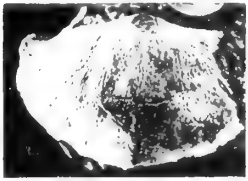

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PLATE 9

Eoplectodonta penkillensis (Reed)

Llandovery, Telychian, Uzmaston Beds, 100 yards NW of Haroldston St. Issels Church, near Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9636 1409. O. T. Jones Collection.

FIG. 1. GSM 37557. Pedicle internal mould, figured Jones 1928 pl. 23, fig. 15 as *Sowerbyella millinensis*. × 4.1.

FIGS. 2, 5. GSM 37559. Latex cast and internal mould of brachial valve, figured Jones 1928, pl. 23, fig. 16 as *Sowerbyella millinensis*. × 5.7 and 4.2.

FIG. 4. GSM 37556. Brachial external mould. × 4.4.

Llandovery, Telychian, Canaston Beds, road cutting opposite Canaston Farm, near Narberth, Pembrokeshire, Wales. Grid Ref. SN/0697 1483.

FIG. 3. GSM 37531. External mould of brachial valve, figured Jones 1928, pl. 23, fig. 22 as the holotype of *Sowerbyella millinensis* var. *canastonensis*. O. T. Jones Collection. × 2.6.

FIG. 6. GSM 37531 (another specimen on the same slab as the last). Internal mould of pedicle valve, figured Jones 1928, pl. 23, fig. 21 as *Sowerbyella millinensis* var. *canastonensis*. O. T. Jones Collection. × 5.1.

FIGS. 7, 10. BB 32418. Latex cast and internal mould of brachial valve. Author's Collection. × 2.6 and 2.8.

Llandovery, Telychian, Uzmaston Beds, near ruins of mill, 200 yds W. by N. of Millin Farm, 3 miles ESE of Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9943 1418.

FIG. 9. GSM 37540. External mould of brachial valve, figured Jones 1928, pl. 23, fig. 18 as the holotype of *Sowerbyella millinensis* var. *parabola*. O. T. Jones Collection. × 3.0.

FIGS. 8, 11. BB 32419. Internal mould of brachial valve. Author's Collection. × 4.0 and 4.4.

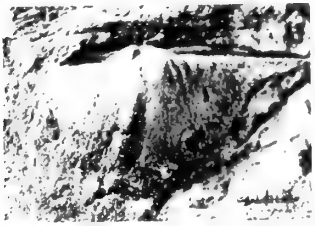
FIG. 12. GSM 37541. Internal mould of pedicle valve, figured Jones 1928, pl. 23, fig. 20 as *Sowerbyella millinensis* var. *parabola*. O. T. Jones Collection. × 1.6.

Llandovery, Telychian, Canaston Beds, South bank of the Eastern Cleddau, Pembrokeshire, Wales. Grid Ref. SN/0485 1385. Author's Collection.

FIG. 13. BB 32226. External mould of brachial valve. × 3.7.

FIG. 14. BB 31839. Internal mould of brachial valve, with conjoined pedicle valve. × 2.0.

FIG. 15. BB 32227. External mould of brachial valve, with conjoined pedicle valve, showing the interarea. × 3.8.



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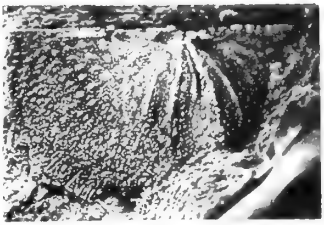

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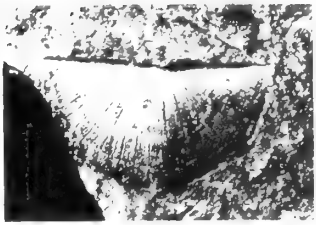

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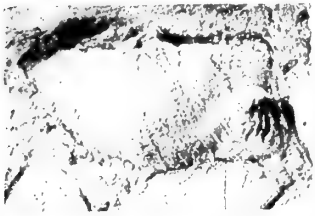

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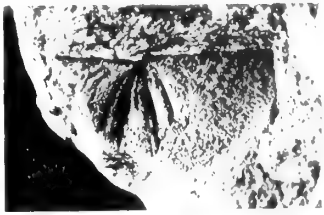

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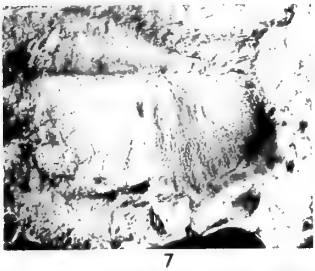

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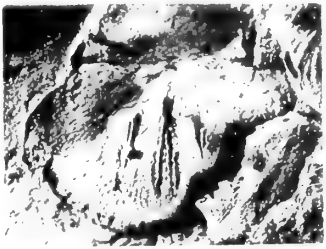

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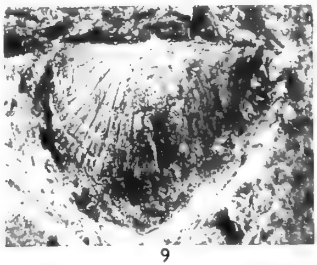

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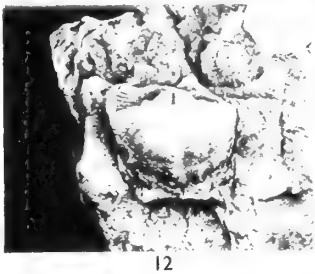

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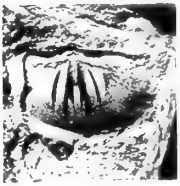

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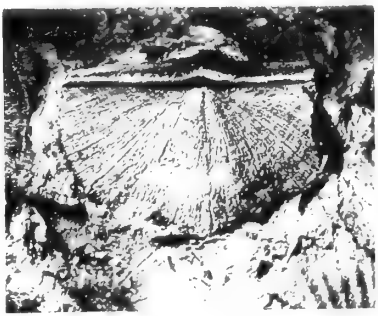

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PLATE 10

Eoplectodonta penkillensis (Reed)

Llandovery, Telychian, Canaston Beds, south bank of the Eastern Cleddau, Pembrokeshire, Wales. Grid Ref. SN/0485 1385. Author's Collection.

FIG. 1. BB 32228. Internal mould of pedicle valve. × 3.5.
FIG. 2. BB 32219. Internal mould of pedicle valve. × 4.2.
FIG. 3. BB 32221. Internal mould of pedicle valve. × 4.0.

Llandovery, Fronian, Pentamerus Beds, Hurst Coppice, Shropshire, England. Grid Ref. SJ/6271 0585. W. F. Whittard Collection.

FIG. 4. BB 32231. Internal mould of brachial valve. × 4.8.

Llandovery, Fronian, Pentamerus Beds, stream exposure in Harper's Dingle, Shropshire, England. Grid Ref. SJ/6314 0669. W. F. Whittard Collection.

FIG. 5. BB 31841. Exterior of pedicle valve. × 2.0.

Llandovery, Lower Telychian, Pentamerus Beds, stream exposure in Sheinton Brook, SE of Cressage, Shropshire. Grid Ref. SJ/6116 0310. Author's Collection.

FIG. 6. OUM C14337. Internal mould of pedicle valve. × 4.0.
FIG. 10. OUM C14396. Internal mould of brachial valve. × 4.0.

Llandovery, Lower Telychian, Hughley Shale, river bank above the unconformity with the Ordovician, Onny River, Shropshire, England. Grid Ref. SO/4260 8532. Author's Collection.

FIGS. 7, 8. OUM C11970. External and internal moulds of a brachial valve. × 4.0.
FIG. 9. OUM C11965. Internal mould of brachial valve. × 3.0.
FIGS. 11, 12. OUM C11962. External and internal moulds of a brachial valve. × 5.0.

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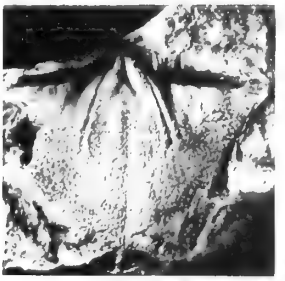

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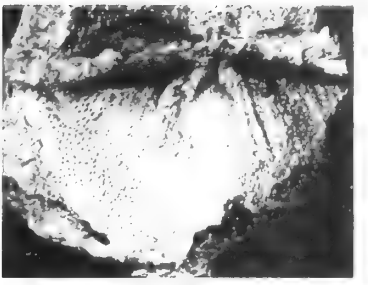

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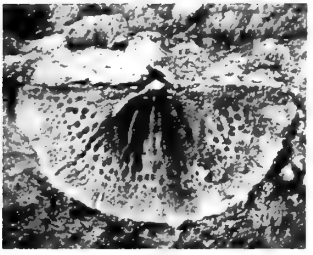

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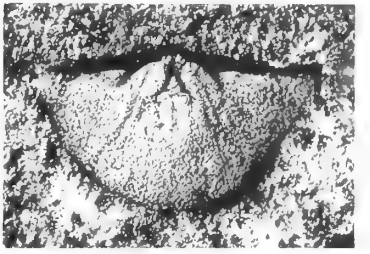

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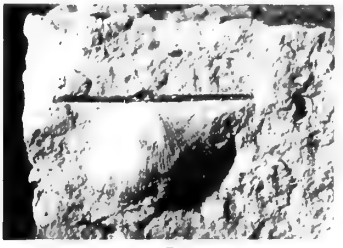

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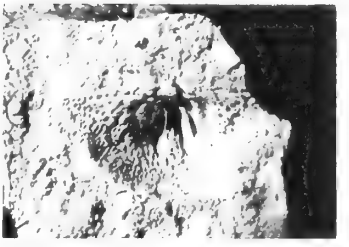

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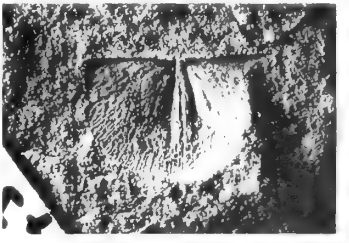

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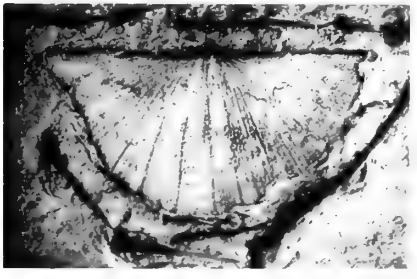

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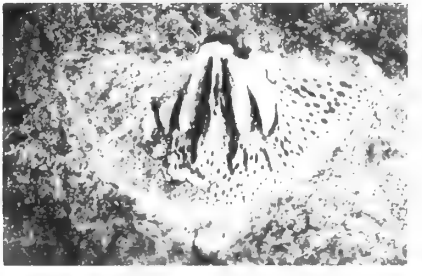

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PLATE 11

Eoplectodonta penkillensis (Reed)

Llandovery, Telychian, stream exposure near Domas, Shropshire, England. Grid Ref. SJ/5936 0062. Author's Collection.

FIG. 1. OUM C13614–5. Slab with three pedicle internal moulds and two brachial external moulds. At the top is a fragment of *Amphistrophia whittardi* Cocks. × 1.3.

FIG. 2. BB 32222. Internal mould of brachial valve. × 4.8.

Llandovery, Telychian, Hughley Shale, stream exposure near Hughley, Shropshire, England. Grid Ref. SO/5605 9747. Author's Collection.

FIG. 3. OUM C13700. Internal mould of pedicle valve. × 4.4.

FIG. 4. BB 31840. Exterior of pedicle valve. × 2.2.

FIG. 7. BB 31838. Exterior of pedicle valve. × 2.2.

Llandovery, Telychian, Wych Beds, bank on south side of football pitch at Cowleigh Park, Malvern Hills, Herefordshire, England. Grid Ref. SO/7616 4723. A. M. Ziegler Collection.

FIGS. 5, 8. OUM C4896. Internal mould and latex cast of pedicle valve. × 2.1.

FIGS. 6, 9. OUM C4857. Internal mould and latex cast of brachial valve. × 3.7.

FIG. 10. OUM C4859. External view of part of a brachial valve, showing the ornament. Many of the moulds of exteriors at this locality do not show any ornament, this is due to the mode of preservation only, as can be seen from this specimen. × 2.5.

FIG. 11. OUM C4872. Internal mould of brachial valve. × 1.9.

FIG. 12. OUM C4890. Internal mould of pedicle valve. × 2.0.

FIG. 13. OUM C4863. Internal mould of brachial valve. × 2.0.

Llandovery, Fronian, " Camregan Group ", Bargany Pond Burn, near Girvan, Ayrshire, Scotland. Grid Ref. NX/2500 9858. Mrs. R. Gray Collection.

FIG. 14. B 44710. Partly exfoliated exterior of pedicle valve, figured Reed 1917, pl. 16, fig. 3, as *Plectambonites transversalis* var. *penkillensis*. Selected lectotype in this paper. × 2.0.

FIG. 15. B 44711. External mould of brachial valve, figured Reed 1917, pl. 16, fig. 4. × 3.5.

FIG. 16. B 44712. Internal mould of pedicle valve, figured Reed 1917, pl. 16, fig. 5. × 2.3.

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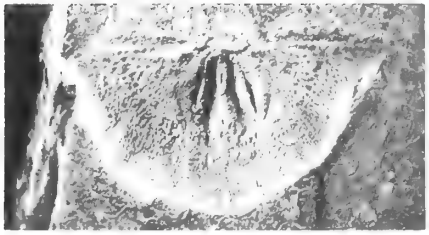

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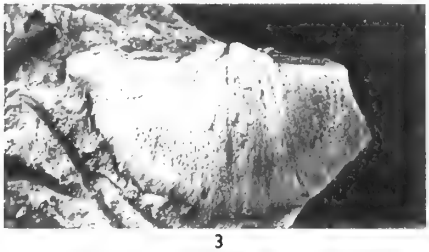

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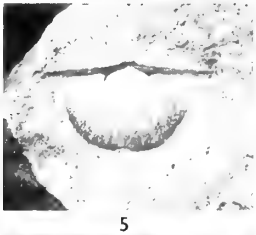

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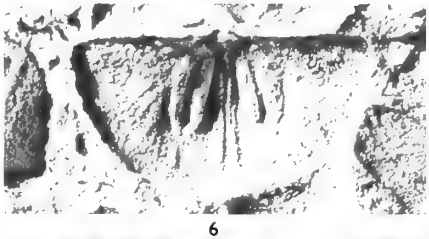

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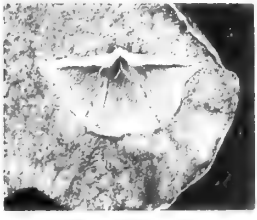

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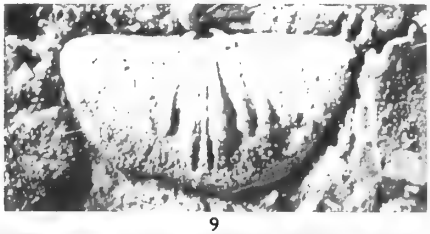

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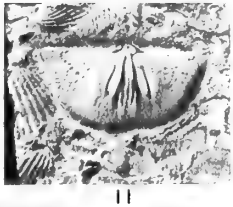

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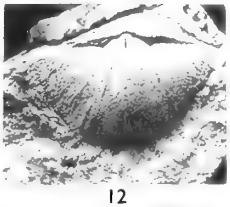

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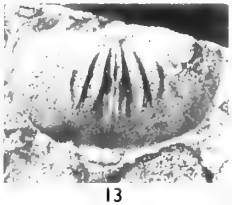

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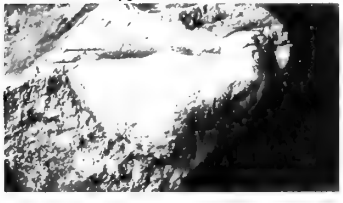

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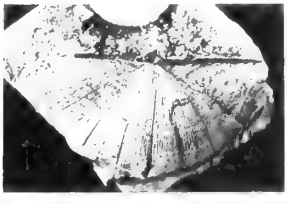

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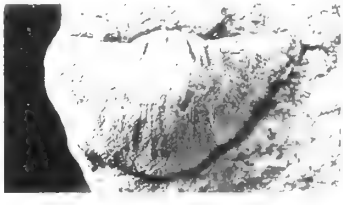

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PLATE 12

Eoplectodonta transversalis (Wahlenberg)

Llandovery, Telychian, Lower Visby Marl, the specimens labelled " Lundbjars " from beach exposure, 1 km west of Lundbjars, Gotland, Sweden. Grid Ref. CK/465 062. The specimens labelled " Nyhamn " are from beach exposure north of Nyhamn, Gotland, Sweden. Grid Ref. CK/663 055. Author's collection.

FIGS. 1–3. RMS Br 102394. Three views of conjoined valves, neotype. × 3.0. Lundbjars.

FIGS. 4, 5. BB 32420. Views of a brachial valve from above and behind. × 3.0 and 2.0. Lundbjars.

FIG. 6. BB 32425. Interior view of brachial valve, showing encrusting rim of polyzoa round the anterior margin. × 3.0. Nyhamn.

FIG. 7. BB 32426. Interior view of brachial valve. × 3.0. Nyhamn.

FIG. 8. BB 32421. Interior view of brachial valve. × 3.0. Lundbjars.

FIG. 9. BB 32427. View of conjoined valves. × 3.0. Nyhamn.

FIG. 10. BB 32428. Interior view of pedicle valve. × 2.5. Nyhamn.

FIG. 11. BB 32422. View of conjoined valves. × 3.0. Lundbjars.

FIG. 12. BB 32423. Interior view of pedicle valve. × 3.0. Lundbjars.

FIG. 13. BB 32424. Interior view of pedicle valve. × 5.0. Lundbjars.

Eoplectodonta duvalii (Davidson)

Wenlock, Slite Marl, ditch in coppice 1.6 km south of Västergarn, Gotland, Sweden. Grid Ref. CJ/292 688. Author's collection.

FIGS. 14, 15. BB 31837. Views of a brachial valve from above and behind. × 3.0.

FIG. 16. BB 32429. View of conjoined valves. × 3.0.

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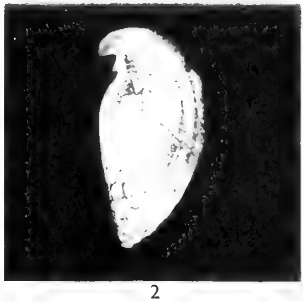
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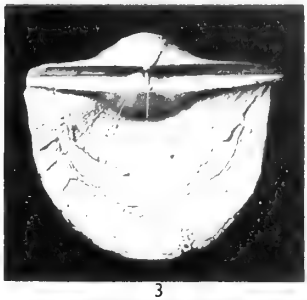
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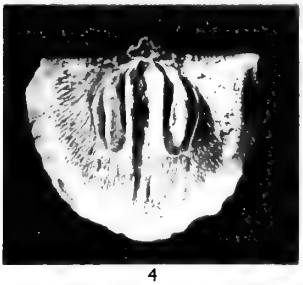
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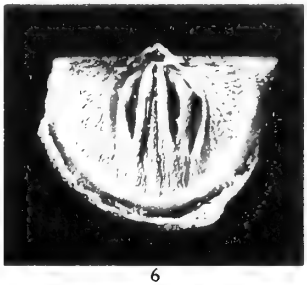
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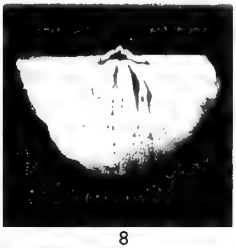
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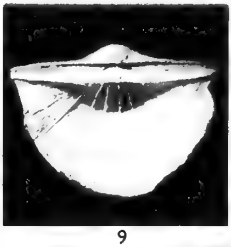
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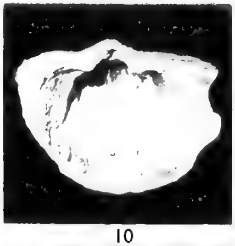
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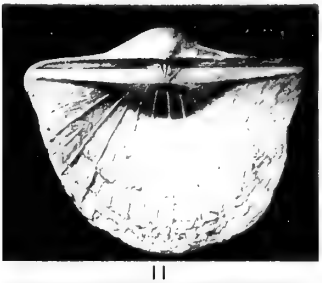
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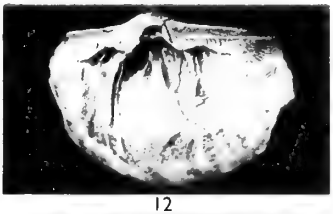
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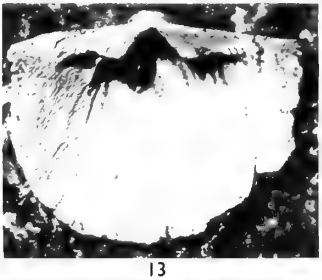
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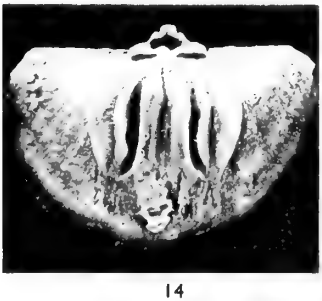
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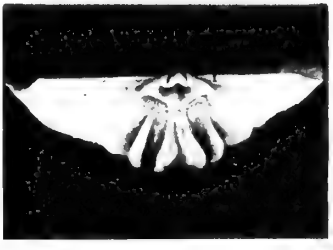
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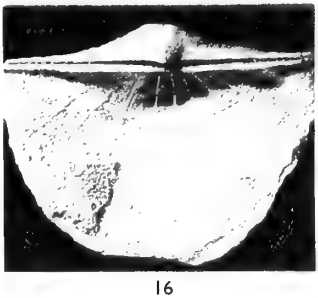
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PLATE 13

Eoplectodonta aff. ***duvalii*** (Davidson)

Wenlock, Upper Visby Marl, no precise locality except Gotland, Sweden. Old collection curated by Lindström.

FIG. 1 RMS Br 31048. Interal view of brachial valve. × 2.8.

Eoplectodonta sowerbyana (Barrande)

Wenlock, Upper Liteň Formation, locality " Hlink ", near Svaty Jan pod Skalou, Bohemia, Czechoslovakia. Author's collection.

FIGS. 2, 4. BB 32415. Pedicle internal mould, viewed from above and behind. × 4.0.

FIG. 5. BB 32413. Internal mould of brachial valve. × 3.3.

FIG. 6. BB 32414. Internal mould of pedicle valve. × 1.7.

FIG. 8. BB 32412. Internal mould of brachial valve. × 3.00, with the median septum clearly visible.

FIG. 9. BB 32411. Latex cast of brachial internal mould. × 1.9.

Eoplectodonta aff. ***duvalii*** (Davidson)

Wenlock, Kitaigorod Formation, Restevo Beds, left bank of the Ternava River, Kitaigorod Village, Podolia, U.S.S.R. Collected by Dr. P. T. Warren, 1968.

FIG. 3. GSM FOR L 64. External view of pedicle valve. × 3.3.

Eoplectodonta duvalii (Davidson)

Lower Wenlock, Buildwas Beds, north bank of River Severn, Shropshire, England. J. Gray Collection.

FIG. 7. GSM 12697. External view of pedicle valve of a pair of conjoined valves. Figured Jones 1928, pl. 24, fig. 2 as the holotype of *Sowerbyella transversalis* var. *lata*. × 2.0.

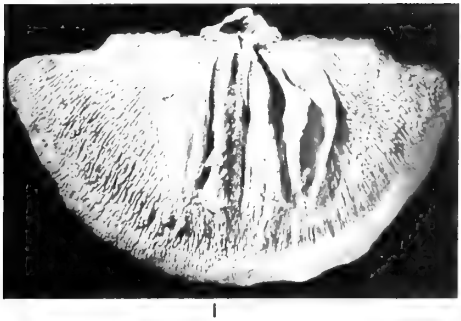
Wenlock Shale, Walsall, Staffordshire, England. T. Davidson Collection.

FIG. 10. B 13730. Pedicle valve embedded in matrix. Holotype, figured Davidson 1847, pl. 12, figs. 20, 21 and refigured Davidson 1848 and 1871. × 2.4.

? Ygerodiscus cornutus (Davidson)

Middle Wenlock, Wenlock Shale, " half a mile west of Buildwas Abbey ", Shropshire, England. T. Davidson Collection (from the washings by G. Maw).

FIGS. 11, 12. BB 32416. Views of conjoined valves from above and below, lectotype. × 4.6.



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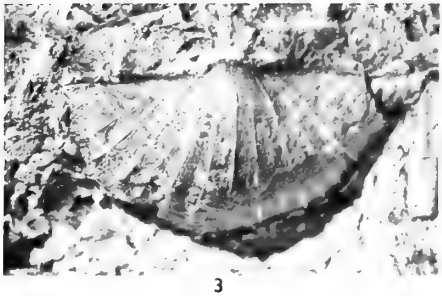

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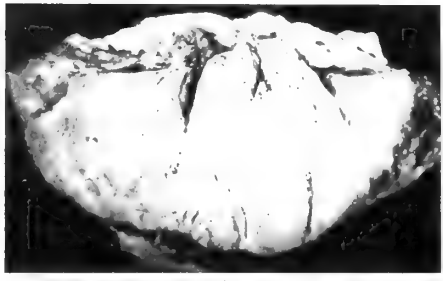

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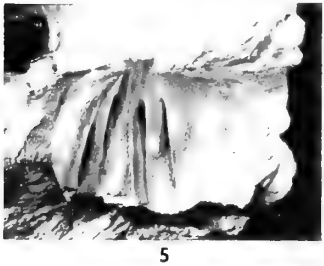

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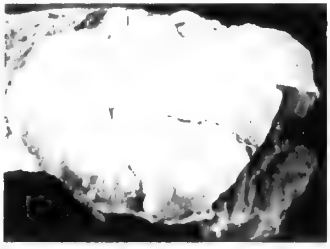

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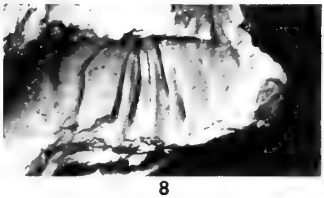

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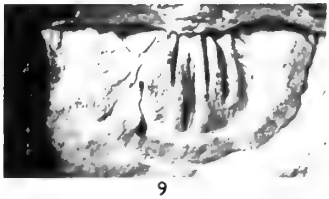

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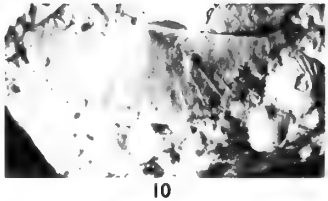

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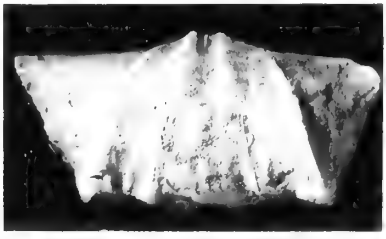

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PLATE 14

? Ygerodiscus cornutus (Davidson)

Middle Wenlock, Coalbrookdale Beds, " half a mile west of Buildwas Abbey ", Shropshire, England. Davidson Collection (from the washings by G. Maw).

FIGS. 1, 2. B 5828. Views of conjoined valves from above and below. × 6.5.

Ygerodiscus undulatus (Salter)

Llandovery (late Idwian or early Fronian), Rosemarket Beds, old quarry, 700 yards south of Bullford, near Haverfordwest, Pembrokeshire, Wales. Grid ref. SM/9218 0980. O. T. Jones Collection.

FIGS. 3, 4, 6, 7. GSM 37560–1. Latex casts and natural moulds of the exterior and interior of a brachial valve, the holotype of *Sowerbyella compressa*, figured Jones 1928, pl. 24, figs. 12 and 13. Despite being registered separately and only the exterior being designated as the holotype, the two specimens are part and counterpart. × 5.0, 3.5, 6.0 and 5.0.

FIGS. 5, 8. GSM 37562–3. External and internal moulds of a brachial valve, figure 5 also shows part of the exterior of the pedicle valve, which is gaping wide open from the brachial valve. Figured Jones 1928, pl. 24, figs. 10, 11, and selected here as lectotype of *Sowerbyella plicata* Jones. Despite the separate registrations, the two specimens are part and counterpart. × 3.1 and 4.4.

FIGS. 9, 11. GSM OTJ1030. Internal mould of brachial valve and latex cast of it. × 5.0.

Landovery, Fronian, C_1 beds, " near footbridge " (now disappeared) River Sefin, south of Lletty'rhyddod, Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7418 2817. Author's collection.

FIGS. 10, 12. BB 32417. Latex cast of internal mould and external mould of a brachial valve. × 5.5 and 6.0.

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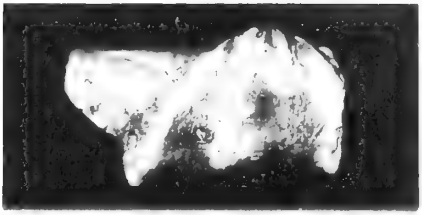

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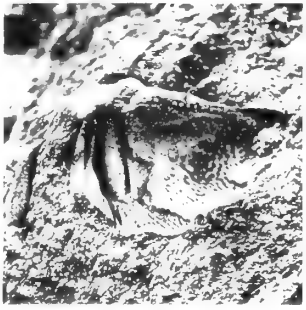

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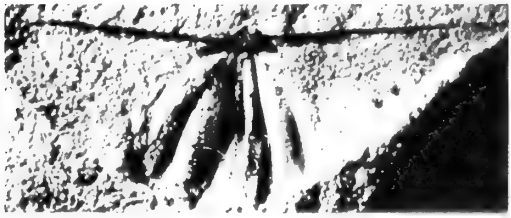

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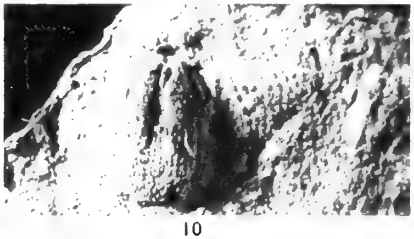

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PLATE 15

Ygerodiscus undulatus (Salter)

Llandovery, probably Idwian, but may be late Rhuddanian, " Mathyrafal ", Meifod, Montgomeryshire, Wales. M'Coy Collection.

FIG. 2. SMA 11308. External mould of a brachial valve, figured M'Coy 1852, pl. iH, figs. 31, 31a as *Leptaena quinquecostata*, figured Jones 1928 pl. 24, fig. 7 as the holotype of *Sowerbyella undulata* var. *maccoyi*. × 3.5.

FIG. 5. SMA 11307. External mould of a brachial valve, figured M'Coy 1852, pl. iH, fig. 30 as *Leptaena quinquecostata*, selected as lectotype by Jones 1928 : 455 and figured by him pl. 24, fig. 3. × 2.5.

Llandovery, probably Idwian, but may be late Rhuddanian, east bank of River Banwy, west of Upper Hill Farm, near Meiford, Montgomeryshire, Wales. This is probably the same locality as the one above from which M'Coy collected his specimens labelled " Mathyrafal ". Grid Ref. SJ/1327 1057. Author's collection.

FIG. 1. BB 31669. Internal mould of pedicle valve. × 4.6.

FIG. 4. BB 31919. Internal mould of brachial valve. × 4.0.

FIGS. 7–9. BB 31906. Two views of a pedicle internal mould and a latex cast of it. Figs. 7 and 8 × 6.3, fig. 9 × 5.0.

Llandovery, Idwian, B Beds, exposure on forestry track, northern area, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/8344 3726. Author's collection.

FIG. 3. BB 32109. Internal mould of pedicle valve. × 4.2.

Llandovery, late Idwian or early Fronian, Rosemarket Beds, old quarry, 700 yards south of Bullford, near Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9218 0980.

FIG. 6. GSM OTJ1018. External mould of brachial valve. × 3.0. O. T. Jones Collection.

FIGS. 10–12. BB 32084. Latex cast of external mould and latex cast and internal mould of pedicle valve. Figs. 10, 11 × 4.6, fig. 12 × 5.6. Author's collection.

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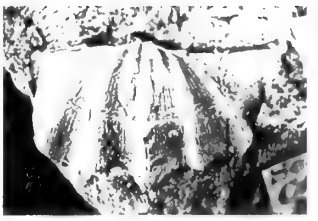

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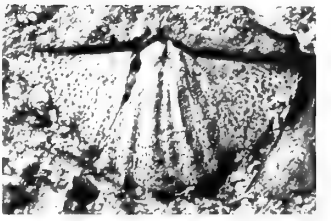

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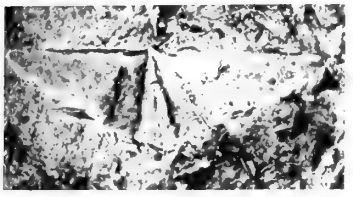

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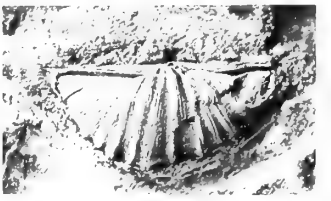

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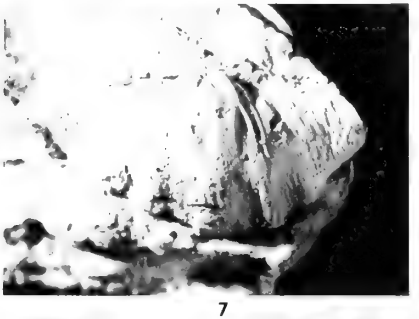

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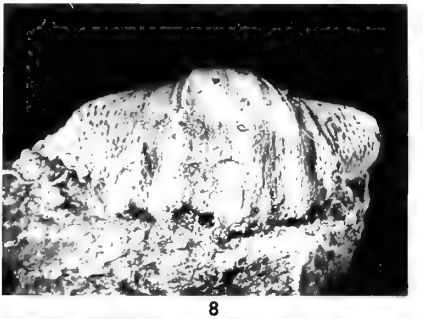

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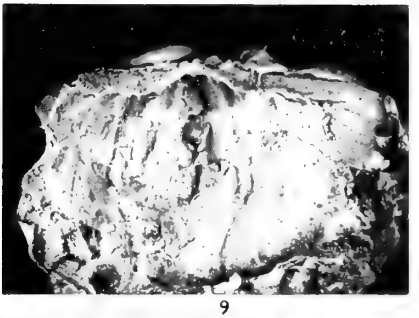

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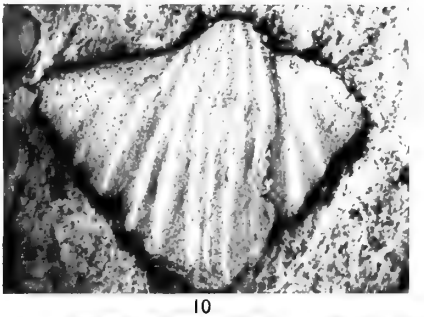

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PLATE 16

Anisopleurella gracilis (Jones)

Llandovery, Rhuddanian, Cartlett Mudstones, south side of railway cutting, 1 mile south of Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/956 146.

FIG. 1. GSM 37554. Specimen showing external mould of the brachial valve in the centre, on which is seen the impression of the outer side septa after presumably post-mortem crushing, with, as an outside rim, part of the internal mould of the pedicle valve. Counterpart to the holotype. O. T. Jones Collection. × 3.4.

FIG. 2. GSM 37552. Internal mould of pedicle valve, showing denticles. Figured Jones 1928, pl. 24, fig. 25. O. T. Jones Collection. × 6.2.

FIG. 3. GSM 37553. External mould of brachial valve, showing impression of outer side septa after crushing and also the conjoined interarea of the pedicle valve. Figured Jones 1928, pl. 24, fig. 24 as a pedicle valve. O. T. Jones Collection. × 4.9.

FIGS. 4, 7. GSM 37551. External mould of pedicle valve and latex cast of it, showing the median septum, inner side septa and outer side septa impressed after crushing. Figured Jones 1928, pl. 24, fig. 23. × 4.5 and 3.5.

FIG. 5. GSM OTJ766. External mould of brachial valve with associated pedicle valve interarea. O. T. Jones Collection. × 3.0.

FIGS. 6, 9. GSM 37555. Brachial valve internal mould and latex cast of it, the internal mould figured Jones 1928, pl. 24, fig. 22. O. T. Jones Collection. × 5.0 and 4.0.

FIG. 8. BB 32052. Latex cast of external mould of pedicle valve, showing impression of brachial valve median septum and both sets of side septa. Author's Collection. × 5.0.

Plectodonta mariae Kozlowski

Lower Devonian, Borszczow Stage, river bank, Krzywce, Podolia, U.S.S.R. (formerly Poland). Kozlowski Collection, in exchange with University of Warsaw 1932.

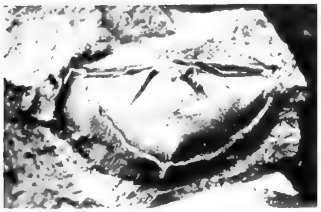
FIGS. 10, 11. B 81371. Two views of a pair of conjoined valves. × 4.4.

FIG. 12. B 81372. Interior of brachial valve. × 8.7.

? *Aegiromena* sp.

Llandovery, Idwian, Newlands Sandstone, near Newlands Farm, Craighead Inlier, near Girvan Ayrshire, Scotland. Grid Ref. NS/2777 0432. E. O. Lundholme Collection.

FIGS. 13, 14. HML 9931. External and internal moulds of a pedicle valve. × 5.8.



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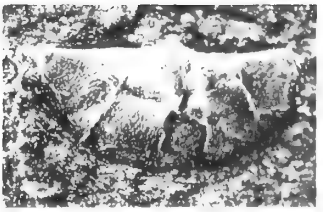

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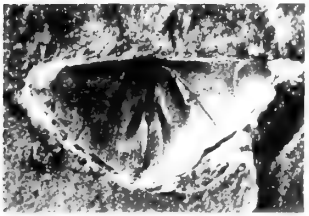

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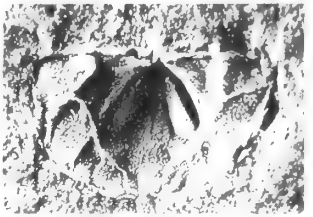

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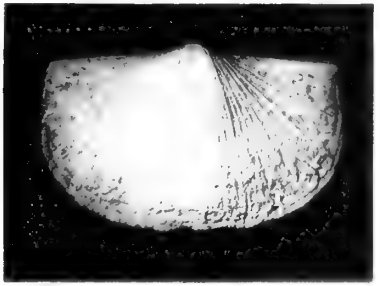

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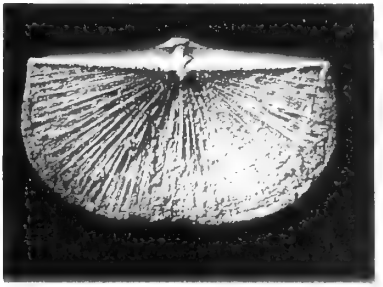

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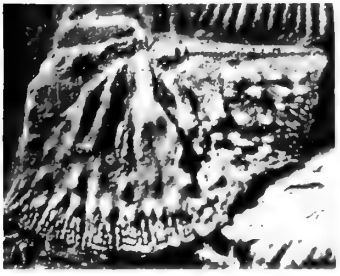

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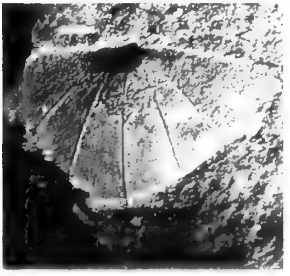

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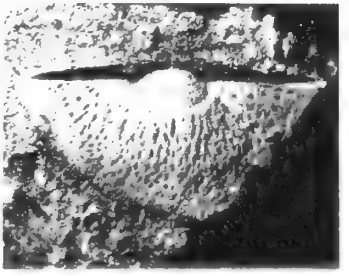

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PLATE 17

Chonetoidea papillosa (Reed)

Ashgill, Slade Beds, quarry at Upper Slade, near Haverfordwest, Pembrokeshire, Wales. Turnbull Collection.

FIG. 1. SMA 11311. Interior of brachial valve, lectotype, figured Reed 1905, pl. 23, fig. 13 and Jones 1928, pl. 25, fig. 21. × 10.

FIG. 2. SMA 11313. Interiors of both brachial and pedicle valves, syntype, figured Reed 1905, pl. 23, fig. 15 and Jones 1928, pl. 25, fig. 24. × 4.0.

FIG. 3. SMA 30841. Exterior mould of pedicle valve. × 4.2.

Aegiria garthensis (Jones)

Llandovery, Rhuddanian, " north of Garth ", Breconshire, Wales. G. Andrew Collection.

FIGS. 4 and 7. GSM 50417 and 50418. Exterior and interior moulds of a brachial valve. Despite different registration numbers, these are part and counterpart. Fig. 4 × 4.0 and fig. 5 × 7.0.

FIGS. 5 and 6. GSM 37589 and 37590. Exterior and interior moulds of a brachial valve. Holotype, figured Jones 1928, pl. 25, figs 2, 26. Despite different registration numbers, these are part and counterpart. × 6.0.

Aegiria grayi (Davidson)

Llandovery, Telychian, Hughley Shales, stream bank at Domas, near Harley, Shropshire, England. Grid Ref. SJ/5936 0062. Author's Collection.

FIG. 8. OUM C13973–5. External moulds (to left and right) and conjoined valves (centre). × 9.0.

Wenlock, Dudley Limestone, Staffordshire, England.

FIG. 9. B 780. Conjoined valves, lectotype. × 8.3. John Gray Collection.

FIG. 10. B 23205. Many conjoined valves. × 4.0. Caroline Birley Collection.

Llandovery, late Fronian or early Telychian, north bank of River Onny, Shropshire, England. Grid Ref. SO/4260 8532. Author's collection.

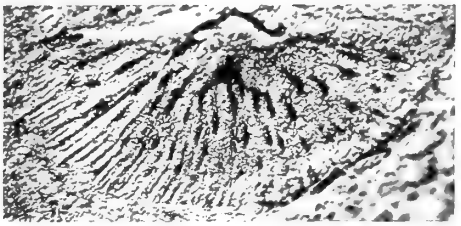
FIG. 11. OUM C12046. Pedicle internal mould. × 10.

FIG. 12. OUM C12051–2. Internal moulds of brachial valves. × 11.

Ludlow, Upper Leintwardinian, Chonetoidea Beds, Pont Shoni, Builth, Radnorshire, Wales. Grid Ref. SO/078 468. Author's collection.

FIG. 13. BB 32430. Pedicle internal mould. × 8.4.

FIG. 14. BB 32431. Brachial internal mould. × 13.



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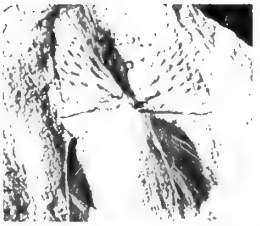

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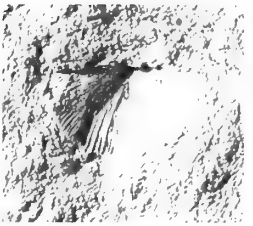

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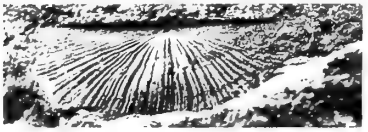

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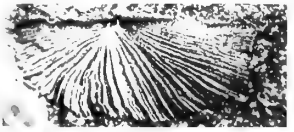

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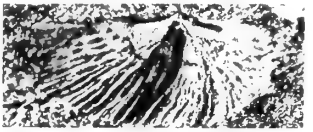

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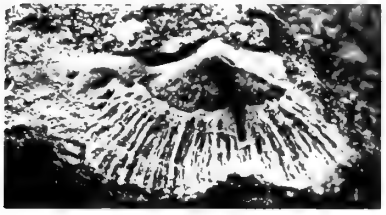

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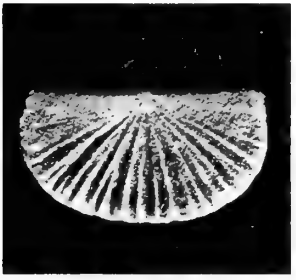

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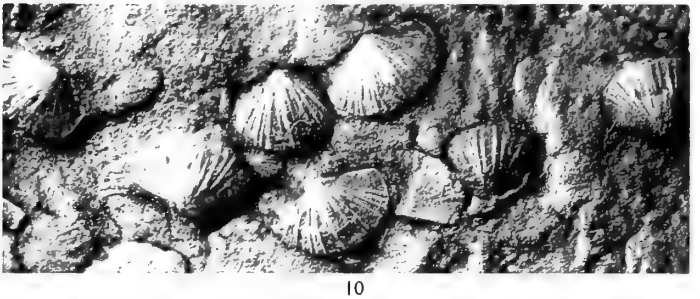

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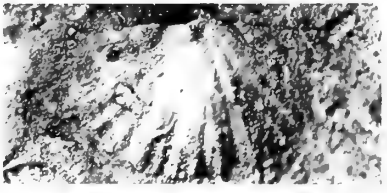

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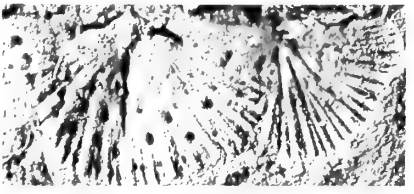

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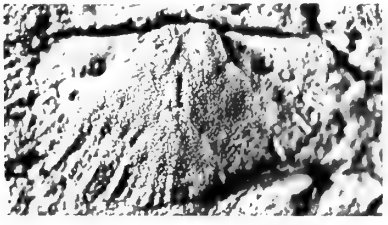

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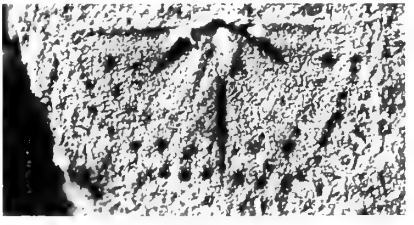

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TWO UPPER CRETACEOUS SALMONIFORM FISHES FROM THE LEBANON

BRITISH MUSEUM
- 5 JAN 1971
NATURAL HISTORY

C. PATTERSON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 19 No. 5
LONDON: 1970

TWO UPPER CRETACEOUS SALMONIFORM FISHES FROM THE LEBANON

BY
COLIN PATTERSON

Pp. 205–296 ; 5 *Plates*, 48 *Text-figures*

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THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 19 No. 5
LONDON : 1970

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THE BRITISH MUSEUM (NATURAL HISTORY)

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TWO UPPER CRETACEOUS SALMONIFORM FISHES FROM THE LEBANON

By C. PATTERSON

CONTENTS

		Page
I.	Introduction	208
II.	Material and methods	208
III.	Description	209
	(a) General	209
	(b) Systematic	209
	Gaudryella gen. nov.	210
	G. gaudryi (Pictet & Humbert)	210
	Humbertia gen. nov.	231
	H. operta sp. nov.	232
IV.	Discussion	250
	(a) Similarities between *Gaudryella* and *Humbertia* and evidence of euteleostean relationships	250
	(b) Differences between *Gaudryella* and *Humbertia* and relationships within the Euteleostei	252
	(i) Ethmoid region	259
	(ii) Jaws and dentition	265
	(iii) Hyoid and branchiostegals	268
	(iv) Caudal skeleton	269
	(v) Conclusions	278
	(c) Comparisons with *Clupavus* and the Clupavidae	283
	(d) Comparisons with other Cretaceous teleosts	288
V.	Summary	290
VI.	References	291
VII.	Abbreviations used in figures	296

SYNOPSIS

Two small, unspecialised teleosts, *Gaudryella* gen. nov. *gaudryi* (Pictet & Humbert) and *Humbertia operta* gen. & sp. nov., are described in detail on the basis of abundant acid-prepared material from the Middle Cenomanian fish beds of Hakel and Hajula, Lebanon. These fishes are superficially very similar, but differ in many anatomical features, some of considerable importance. Despite these differences, it is not possible to show that either species is more closely related to any living or Cretaceous fish than is the other. The only group with which they show positive evidence of relationship is the salmoniform subgroup containing the Osmeroidei and Stomiatoidei, especially the hypomesine osmerids, but these relationships are not sufficiently close to place either genus in one of these suborders, and they are left as Salmoniformes *incertae sedis*. The Upper Jurassic and Cretaceous family Clupavidae is reviewed and is found to contain poorly known, superficially similar species whose relationships are largely unknown. The ethmoid ossifications of teleosts and the caudal skeletons of eutelosts are discussed, and a hypothesis of euteleostean interrelationships is suggested on evidence from the caudal skeleton.

I. INTRODUCTION

THIS paper contains detailed accounts of two superficially similar, *Clupavus*-like teleosts, with a discussion of their relationships and of the status of the family Clupavidae. In 1967 I published " preliminary reconstructions " of the skull and caudal skeleton of " an as yet undescribed species of *Clupavus* " from the Cenomanian fish beds outcropping at Hakel and Hajula in the Lebanon (Patterson 1967b, figs. 9–11; see also Patterson 1967a : 72). These reconstructions were made in order to demonstrate that the genus *Clupavus* Arambourg and the family Clupavidae, as then understood, were not close relatives of the clupeomorph fishes, with which they had previously been placed. Recently I took up the material of this " *Clupavus* sp. " again in order to prepare a detailed description. After making transfer preparations of more specimens and puzzling over the available material for several weeks, I eventually realized that it was not conspecific : two species are present, superficially very similar, of which one is abundant and the other relatively rare, and while my preliminary restorations of the skull were based almost entirely on the commoner form, the restoration of the caudal skeleton was a composite of the two. Once I had learned to distinguish these two species, and had obtained more specimens of the rarer species from the large collection of fishes from Hajula in the American Museum of Natural History, New York, I found that the differences between the two are rather profound. They are described below as different genera, but their relationship is almost certainly more distant. The problem of assessing the significance of the similarities and differences between these two Cretaceous species, both in regard to their interrelationships and their relationships with contemporary and living teleosts, raises various questions concerning the evolution and structure of the Euteleostei, which are discussed below. This is the second of a series of papers based primarily on material collected by the author in the Lebanon in 1964.

I am indebted to Dr. Bobb Schaeffer, American Museum of Natural History, and to Prof. Camille Arambourg and Mlle Jean Signeux, Museum d'Histoire Naturelle, Paris, for the loan of specimens, and to Sci. mag. Niels Bonde, Copenhagen, for information about various clupavid specimens in European museums. I am most grateful to Dr. P. H. Greenwood and Dr. D. E. Rosen for valuable discussions and advice, to Dr. S. H. Weitzman for reading and commenting on the manuscript, and to Mr. C. I. Macadie for introducing me to the value of radiographs of transfer preparations. The photographs were taken by Mr. T. W. Parmenter.

II. MATERIAL AND METHODS

The fossil material described here is in the collections of the British Museum (Natural History), designated by register numbers with the prefix ' P. ' or without prefix, and the American Museum of Natural History, referred to by the prefix ' AM '.

The descriptions are based almost entirely on acid prepared specimens, since the two genera are often extremely difficult to distinguish in unprepared material. Specimens were prepared by the transfer technique (Toombs & Rixon 1959)—etching away the matrix after embedding the fossil in epoxy resin—and a few skulls were prepared as free-standing objects by solution of the matrix from specimens in which the head was still unexposed. After study of enough of these preparations to

gain familiarity with the various bones of the two species, a good deal of valuable material was obtained by acid treatment of random blocks of rock from Hajula and sorting of the isolated bones in the residues. This method was particularly useful with *Gaudryella gaudryi*, since this is the most abundant fish at Hajula.

Radiographs of transfer preparations are sometimes very valuable, revealing features not visible by direct examination (cf. Pls 1, 3–5), and radiography is worth considering as a standard technique with all such preparations. Crude but useful histological study of transfer preparations can be carried out very simply, by partially filling the cavity in the resin block with xylene and examining the fish in transmitted light on the microscope stage.

III. DESCRIPTION

(a) General

The species described below as *Gaudryella* gen. nov. *gaudryi* (Pictet & Humbert) and *Humbertia operta* gen. & sp. nov. are usually to be found in museum collections undetermined or under the names *Scombroclupea gaudryi* and *Scombroclupea* sp. (*Scombroclupea* is a clupeomorph genus, containing fishes easily distinguished from and unrelated to those described here). *Gaudryella gaudryi* and *Humbertia operta* occur at both Hakel and Hajula. Pictet & Humbert (1866) based their species *Clupea gaudryi* on six specimens from Hakel. At Hakel neither species is abundant, but they are probably commoner than their representation in museum collections would lead one to believe since these small, unremarkable looking fishes have not attracted collectors. At Hajula, *Gaudryella gaudryi* is very abundant and is certainly the commonest fish, a position filled at Hakel by the clupeomorph *Diplomystus brevissimus*, which is rare or absent at Hajula. *Humbertia operta* is much less abundant than *G. gaudryi* but is still quite common. The large collection of fishes from Hajula in the American Museum of Natural History (Hay 1903) seems to have been made more or less at random, without selection according to the size, distinctiveness or rarity of the fossils. A sample of 72 '*Scombroclupea* sp.' from this collection contained 17 *Humbertia operta* and 55 *Gaudryella gaudryi*, a ratio of about 25% : 75%, which is probably a fairly good estimate of their relative abundance. From Hakel, a much smaller sample is available, but the BM(NH) has six *Gaudryella gaudryi* and two *Humbertia operta*, indicating, probably by chance, exactly the same proportions.

There is no apparent ecological difference between *Gaudryella* and *Humbertia*, since at Hajula specimens of the two sometimes occur side by side on the same bedding plane. *Gaudryella gaudryi* was possibly a shoaling fish, since several individuals often occur on one bedding plane. *Humbertia operta* was more probably solitary, since no such multiple occurrences are known.

(b) Systematic

Division *TELEOSTEI* (*sensu* Nelson 1969a)
Cohort *EUTELEOSTEI* (Greenwood *et al.*, 1967)
Superorder PROTACANTHOPTERYGII (Greenwood *et al.*, 1966)
Order SALMONIFORMES
Suborder and family ***incertae sedis***

Gaudryella gen. nov.

DIAGNOSIS. Small, slender, round-bodied salmoniform fishes ; parietals in contact medially and bearing the supratemporal commissure, post-temporal fossa roofed ; nasals short and trough-like ; rostral and mesethmoid separate, rostral much as in *Megalops* but without ethmoid commissure, mesethmoid ossified endo- and perichondrally ; vomer toothed and with long posterior process, parasphenoid toothless and without basipterygoid process ; occipital condyle formed by basioccipital only, intercalar small, otolith chamber not inflated, orbitosphenoid and basisphenoid present, sclerotic ossified; large supraorbital, antorbital, lachrymal, three infraorbitals and large dermosphenotic present, posterior infraorbitals extending to preopercular, uppermost infraorbital probably representing two fused bones ; hyomandibular vertical, double-headed, quadrate condyle below centre of orbit, metapterygoid reduced, no palatine or pterygoid teeth ; gape small, premaxilla small, simple and toothless, maxilla toothed, curved, not extending to middle of orbit, two mobile supramaxillae ; mandible with long, high coronoid process, dentary with short, steeply ascending oral border, few small teeth, a moderately large pocket on its inner face and the symphysis serrated ; distal ceratohyal perforate, basihyal unossified but heart-shaped basihyal tooth plate present ; 11 branchiostegals, the last two spathiform ; long, toothless gill-rakers on gill arches ; no suprapreopercular, subopercular not enlarged ; about 43 vertebrae, 15 caudal, anterior neural arches autogenous, about 7 supraneurals above anterior vertebrae, simple epineurals and epipleurals on abdominal vertebrae, anterior epineurals fused with neural arches ; mesocoracoid, two postcleithra and several distal pectoral radials present ; pelvics inserted below hind end of dorsal fin and with 12–13 rays, pelvic splint fused with girdle ; dorsal fin short, at mid-point of back, anal small and remote ; PU2 with short, leaf-like neural spine, small lamellar expansions on neural spine of PU3 and haemal spines of PU2-3 ; PU1, U1, stegural, parhypural and lower hypurals fused, U2 separate ; third and fourth hypurals fused, fifth and sixth autogenous ; stegural forked proximally, second uroneural present ; two epurals ; caudal fin forked, 19-rayed, one urodermal and reduced caudal scutes present ; scales large, very thin, cycloid, not extending on to skull or fins, lateral line complete ; skeleton mainly acellular.

TYPE (and only) SPECIES. *Clupea gaudryi* Pictet & Humbert (1866).

Gaudryella gaudryi (Pictet and Humbert)

Pl. 1, figs. 1, 2 ; Pl. 2, fig. 1 ; Pl. 3, fig. 2 ; Pl. 4, fig. 1 ; Pl. 5, fig. 1 ; Figs. 1–14, 30–33.

1866 *Clupea gaudryi* Pictet & Humbert : 60, pl. 5, figs. 2–5.
? 1879 *Clupea gaudryi* Pictet & Humbert ; Bassani : 163.
? 1882 *Clupea gaudryi* Pictet & Humbert ; Bassani : pl. 7, figs. 1–4.
1901 *Scombroclupea gaudryi* (Pictet & Humbert) Smith Woodward : 138, *partim* (specimen 49503 only).
1967a *Clupea gaudryi* Pictet & Humbert ; Patterson : 72.
1967b *Clupavus* sp. Patterson, figs. 9, 10 (*non* fig. 11).

DIAGNOSIS. *Gaudryella* reaching about 90 mm. in standard length ; mean pro-

portions (as % standard length) : total length 116, head length 28, trunk depth 18, predorsal length 44·5, predorsal length 84·5, prepelvic length 58·5 ; 41–44 vertebrae, mean 43 ; D ii, 10 ; A ii, 7 ; P 15–16 ; V 12–13 ; C v–vii, I, 9, 8, I, vii–ix ; 6–8 scales in a transverse series on the trunk, about 45 lateral line scales.

LECTOTYPE. Pictet & Humbert figured three specimens of this species which are in the Musée d'Histoire naturelle, Geneva. The specimen illustrated in pl. 5, fig. 4 is selected as lectotype.

HORIZON AND LOCALITIES. Middle Cenomanian, Hakel and Hajula, Lebanon. Possibly also occurring in the Lower Cenomanian of Lesina, Dalmatia (Bassani 1882 ; see p. 288).

MATERIAL. Six specimens from Hakel in the BM(NH) and numerous specimens from Hajula in the BM(NH) and the American Museum of Natural History, especially the following acid prepared specimens : 49503, P.13875, P.13876, P.48224 (all Hakel), P.9991 (Pl. 2, fig. 1, Figs. 9, 10, 12C, 13A), P.48045, P.48047 (Pl. 1, figs. 1, 2, Fig. 6), P.48048/9, P.48050/1 (Fig. 5), P.48063, P.48065, P.51242, P.51243, P.51244 (Fig. 1), AM 3783 (four individuals together with two disarticulated *Humbertia operta*, Pl. 4, fig. 1), AM 4115 (Pl. 5, fig. 1), AM 4599, AM 5568, AM 5579 (Fig. 14A) (all Hajula) ; and the following isolated bones or parts of the skeleton from Hajula : P.51245–6 (Fig. 2), P.51247–9 (Fig. 3) P.51250 (Fig. 4), P. 51251–3 (Fig. 7), P.51254 (Fig. 8), P.51255–6 (Fig. 11), P.51257 (Fig. 12A,B), P.51258 (Fig. 13B).

REMARKS. As previously noted (Patterson 1967a : 72), the specimens referred to *Scombroclupea gaudryi* by Smith Woodward (1901 : 138) are (except 49503) true *Scombroclupea*, probably *S. macrophthalma*, and are not conspecific with the type material of *Clupea gaudryi*, which lacks the abdominal scutes and anal finlets typical of *Scombroclupea*. D'Erasmo has referred to *Clupea gaudryi* (1922 : 72) and *Scombroclupea gaudryi* (1946 : 70) specimens from the Lower Cenomanian of Comen, near Trieste, which have abdominal scutes, forked intermusculars and anal finlets and are therefore also true *Scombroclupea*. Other specimens referred to this species by Bassani (1879, 1882) and Kramberger (1895) are discussed on p. 288.

DESCRIPTION. (i) *General features*. *G. gaudryi* is a small, slender, round-bodied fish. The largest individuals are about 90 mm. in standard length, but such large specimens are uncommon and the modal standard length is 60–70 mm. The body can have been only slightly laterally compressed since few specimens are preserved in lateral view, the usual mode of preservation of laterally compressed fishes. The dimensions of eight specimens are given in Table 1 : the variability of the proportional measurements is in part due to inaccuracies caused by twisting of the fishes during fossilisation, but the mean of these proportions seems to be fairly accurate.

(ii) *Skull roof and braincase*. The skull roof is partially shown in Figs. 1, 5 and 6, and is restored in Fig. 30. The skull roof is smooth and flat except for the raised tubes containing the sensory canals, and is long, with the anterior part of the frontals and the ethmoid drawn out into a slender snout. The supraoccipital (Soc) is small, with a short, thumb-like crest projecting posteriorly. The epiotics (Epo) border the supraoccipital and bear prominent articular surfaces for the post-temporals. The

parietals (Pa) meet in the mid-line, covering the anterior part of the supraoccipital, and join the epiotics in slightly digitate sutures. Laterally the parietals meet the pterotics (described on p. 216) forming the roof of the post-temporal fossa. There is a shallow transverse groove across the parietal, normally interrupted at a point which seems to be the centre of ossification of the bone. The lateral part of this groove is in line with the medial limb of the supratemporal and must have carried the supratemporal commissure. The medial part of the groove, usually separated from the lateral part and often ' L '-shaped (Fig. 1), may represent the middle pit-line, but it is not possible to be certain of this.

TABLE 1

Proportional measurements of eight specimens of *Gaudryella gaudryi*

Specimen	Standard length, mm.	as % standard length: Total length	Head length	Trunk depth	Predorsal length	Preanal length	Prepelvic length
P.13875 (Hakel)	45	—	30	18	42	84	58
P.13873 (Hajula)	51	118	29	18	45	82	55
P.13876 (Hakel)	54	—	29	20	44	84	56
P.48047 (Hajula)	67	—	28	15	48	87	63
P.46578 (Hakel)	71	—	24	20	42	82	54
P.48045 (Hajula)	72	—	26	18	40	86	56
P.13871 (Hajula)	73	116	30	18	48	85	66
AM 4146 (Hajula)	88	115	26	19	47	86	60
Mean	—	116	28	18	44·5	84·5	58·5

The frontals (Fr ; Fig. 3A) overlap the parietals posteriorly and the autosphenotics postero-laterally. Anteriorly the frontal tapers and ends as a thickened splint with a lamina of thin bone extending medially. The postero-lateral wing of the rostral lies on the upper surface of this lamina, fitting into the angle between it and the lateral, splint-like part (Fig. 1). The supraorbital sensory canal ran within the frontal in tubes which are slightly raised above the surface of the bone. At the postero-lateral corner of the frontal the canal passed out through a large pore and may have anastomosed with the temporal canal on the pterotic. There is a long, slender parietal branch of the canal passing back in a tube which opens at (Fig. 3A) or near (Fig. 1) the posterior margin of the frontal. A short postero-medial branch of the canal opens through a small pore at or just in front of the origin of the parietal branch. The epiphyseal branch passed medially in a tube which opens by a wide pore near the mid-line. There is one pore over the main canal anterior to the

epiphyseal branch. Anteriorly the canal left the frontal above the front of the orbit and passed to the nasal (Na, Figs. 1, 6), a small, trough-like bone.

The long, slender ethmoid region is occupied by the endochondral and perichondral mesethmoid and lateral ethmoids, and the dermal rostral (the homologies of the mesethmoid and rostral are discussed on p. 264). The rostral (Ro ; Figs, 1, 2, 5) is a

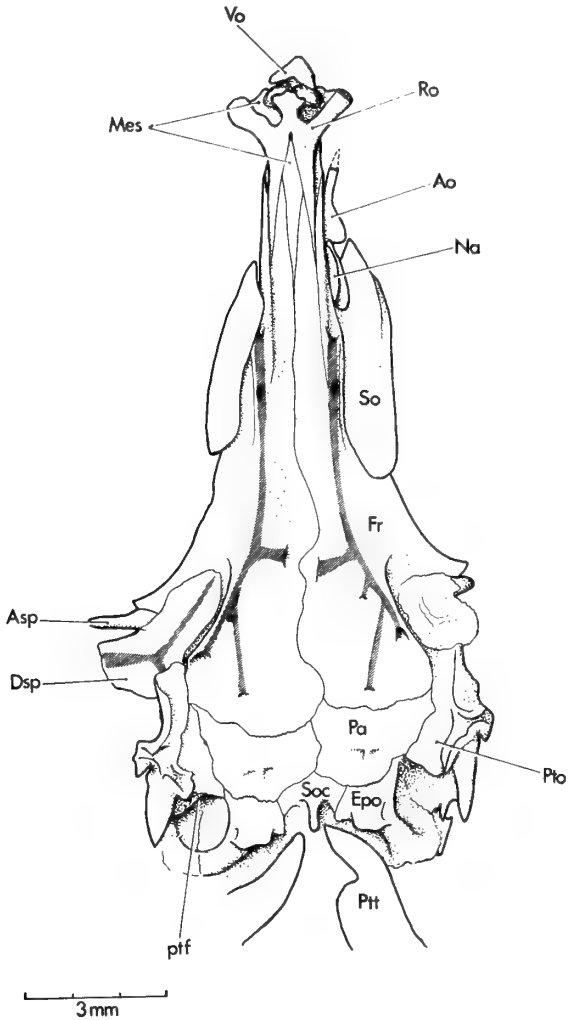

FIG. 1. *Gaudryella gaudryi* (Pictet & Humbert). Skull roof as preserved in P.51244, Hajula, Lebanon. Explanation of abbreviations p. 296.

superficial bone, not fused with the underlying mesethmoid. Anteriorly the bone has a median process and paired ventro-lateral wings, underlain by processes of the mesethmoid. Posteriorly there is a pair of very long, tapering processes which fit in

grooves on the upper surface of the frontal. There is no trace of a rostral commissure or pit-line. The mesethmoid (Mes ; Figs. 2, 5) is an extensive endochondral and perichondral ossification, fitting closely against the underside of the rostral. The perichondral upper surface of the bone (supraethmoid in Weitzman's (1967b) terminology) is exposed between the frontals and the posterior processes of the rostral (Fig. 1). Underneath the median anterior process of the rostral the mesethmoid has a similar but broader anterior process bearing a pair of large facets with which the

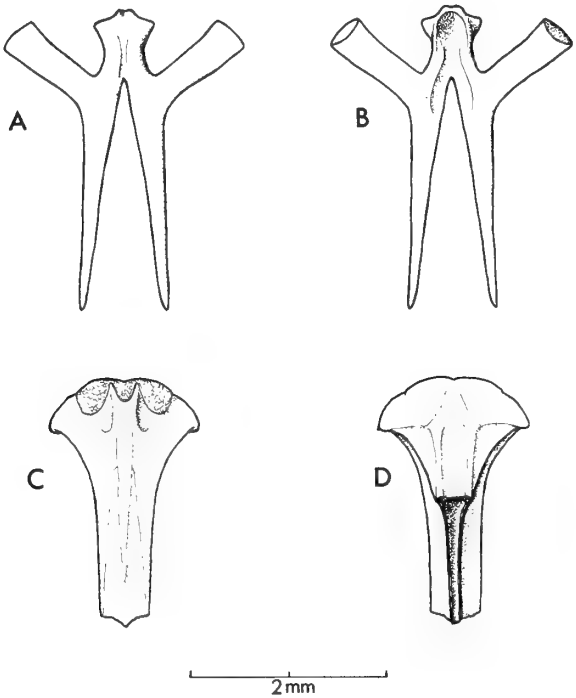

FIG. 2. *Gaudryella gaudryi* (Pictet & Humbert). Isolated rostral (A,B) and mesethmoid (C,D) in dorsal (A,C) and ventral view (B,D). Restorations based on P.51245 (rostral) and P.51246 (mesethmoid), Hajula, Lebanon. The mesethmoid is from a smaller individual than the rostral.

maxillae articulate. Below the ventro-lateral processes of the rostral there are processes of the mesethmoid ending in facets which articulate with the palatine. Posteriorly the mesethmoid extends back as a pair of vertical perichondral laminae which form the medial wall of the nasal capsules (capsular ethmoid bones in Weitzman's terminology). The lateral ethmoids are flimsy perichondral ossifications, usually covered by the large supraorbital.

The vomer (Vo, Figs. 1, 5, 9) is closely applied to the underside of the mesethmoid. Anteriorly the vomer ends in a projecting keel bearing a pair of large articular surfaces for the heads of the maxillae. Posteriorly the vomer has a very long shaft extending

back below the parasphenoid to the level of the centre of the orbit (Figs. 4, 9). Ten to twenty small teeth are borne in a single or partially double row on a median crest on the underside of the vomer. The parasphenoid (Pas ; Fig. 4) is slender and untoothed. At the back of the orbit the parasphenoid broadens and has a large marginal notch for the efferent pseudobranchial artery (epsa), but there is no basipterygoid process. Posteriorly the parasphenoid ends in two wings below the basioccipital, with the posterior opening of the myodome between them.

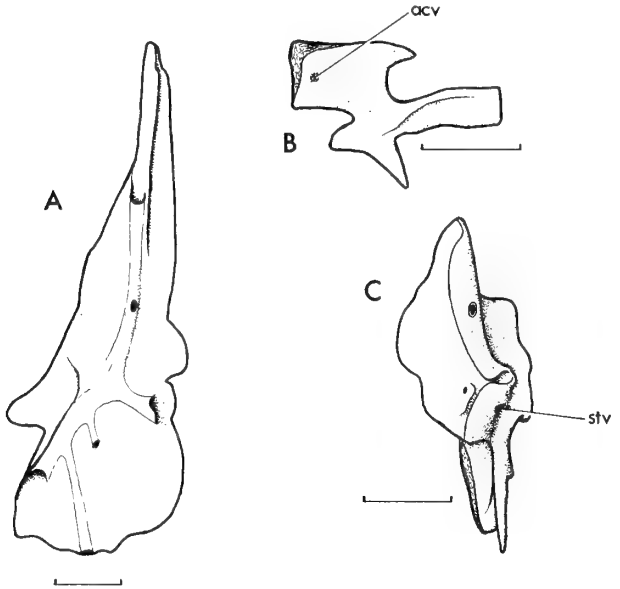

FIG. 3. *Gaudryella gaudryi* (Pictet & Humbert). Isolated left frontal (A, P.51247), orbitosphenoid (B, P.51248) and right pterotic (C, P.51249), from different individuals, Hajula, Lebanon. A,C, dorsal view, B, right lateral. Scale 1 mm. Explanation of abbreviations p. 296.

The endocranium (Fig. 4) is partially visible in several transfer preparations, but is best seen in P.51250, an isolated, crushed braincase, and in AMNH 3783. The endocranium shows no very remarkable features and will be described briefly. The occipital condyle is formed by the basioccipital alone. As noted above, the myodome (myo) opens posteriorly below the occipital condyle. The lateral wall of the saccular chamber is not inflated and there is no fenestra at the junction of the basioccipital (Boc), exoccipital (Exo) and prootic (Pro). The intercalar (Ic) is a small, superficial bone plastered over the junction of the exoccipital and pterotic on the posteroventral angle of the braincase. There is no distinguishable subtemporal fossa, and no forward extension of the intercalar in this region. There is no indication of any association between the swimbladder and the ear, and there are no bullae in the prootic, pterotic or exoccipital. The trigemino-facialis chamber has at least three external openings, with those of the hyomandibular trunk (VII hm) and jugular vein (ptfc) separated by a short jugular canal. The oculomotor nerve passed through a

large foramen in the orbital surface of the prootic, close to its junction with the basisphenoid. The basisphenoid has a long pedicel extending down to the parasphenoid. The articular facet for the hyomandibular (fhm) is clearly divided into two portions, the posterior on the pterotic, the anterior on the autosphenotic : the prootic forms no part of the hyomandibular facet. The autosphenotic (Asp) has a prominent, spine-like postorbital process and is penetrated by a canal for the otic nerve, entering through a large foramen in the orbital surface and emerging in the dilatator fossa (fotn). The dilatator fossa is large and shallow, and is covered by the dermosphenotic : the fossa is excavated in the pterotic posteriorly, the sphenotic ventrally and the frontal anteriorly.

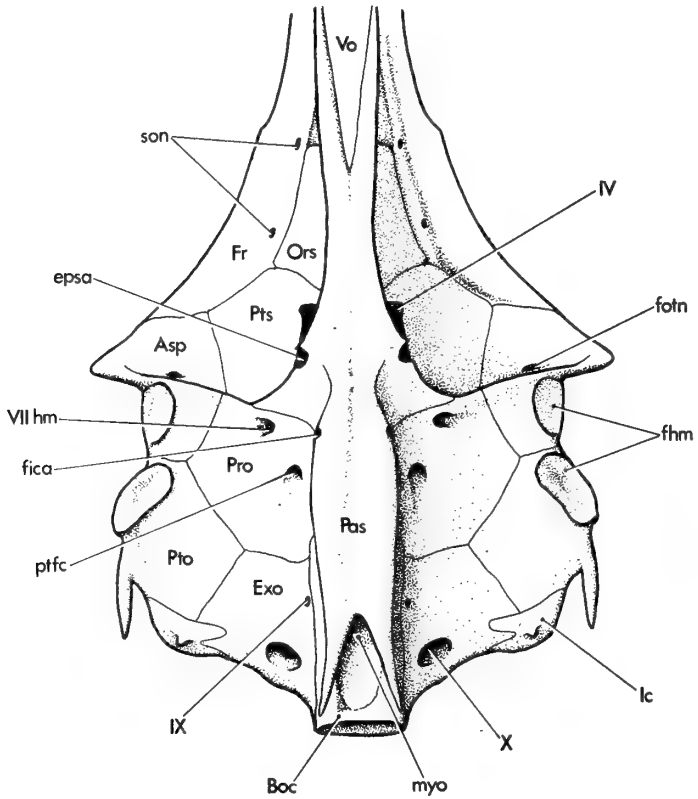

FIG. 4. *Gaudryella gaudryi* (Pictet & Humbert). Neurocranium in ventral view, restoration based on P.51250 and AM 3783, Hajula, Lebanon. × 15 approx. Explanation of abbreviations p. 296.

The autopterotic and dermopterotic are completely fused into a compound pterotic ossification (Pto ; Fig. 3 C) which forms the dorso-lateral and ventro-lateral walls of the roofed post-temporal fossa. The dermal portion of the pterotic carried the temporal sensory canal in a shallow groove which is covered by a flange pro-

jecting from the lateral and posterior margins of the bone : although this covering flange effectively converts the sensory canal groove into a tube, it is open medially throughout its length. Posteriorly the sensory canal passed to the supratemporal, postero-laterally the preopercular canal left through a large groove, and anteriorly the canal passed to the dermosphenotic. If there was an anastomosis between the temporal and supraorbital canals it can only have lain superficial to the antero-medial part of the pterotic : there is no evidence of such an anastomosis on the bones and quite possibly it was not present. There is a small pore in the flange covering the anteriorly directed part of the sensory canal in the pterotic. Immediately behind the posterior, transverse part of the canal there is a large foramen (stv) leading dorso-laterally from the post-temporal fossa which probably transmitted the supratemporal branch of the vagus nerve. Behind this foramen the pterotic bears a long, membranous splint which extended back into the body musculature.

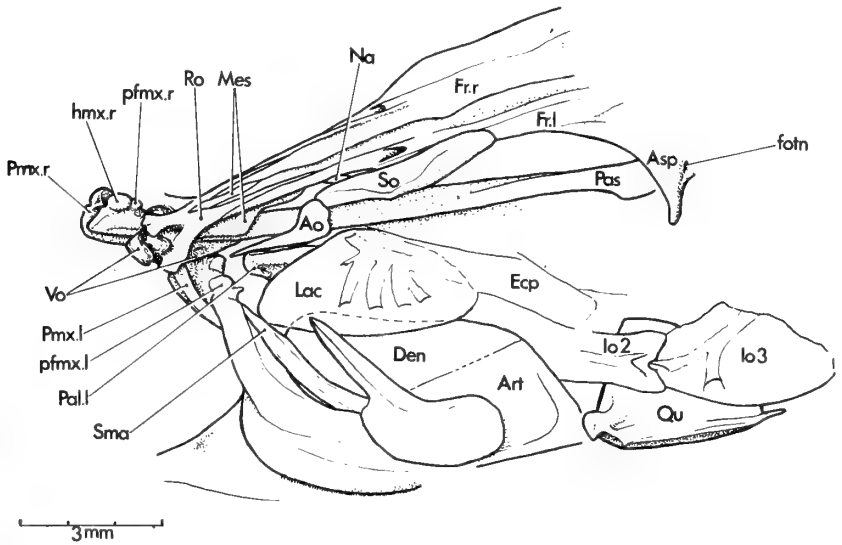

FIG. 5. *Gaudryella gaudryi* (Pictet & Humbert). Anterior part of skull as preserved in P.48051, Hajula, Lebanon. The suffixes ' r ' and 'l ' denote bones of the right and left side, explanation of other abbreviations p. 296.

The pterosphenoids (Pts) do not meet the mid-line and each has a notch in its ventral margin, probably marking the passage of the trochlear nerve (IV). There is a large, median orbitosphenoid (Ors ; Fig. 3B) with an anterior process passing forwards towards the lateral ethmoids below the olfactory nerves, and a stout ventral process extending downwards in front of the optic fenestra. There is a small foramen for the anterior cerebral vein (acv) in the posterior part of the orbitosphenoid. The sclerotic is ossified (scr, Fig. 6), probably in four pieces.

(iii) *Circumorbital bones.* The orbit is surrounded by seven bones, the dermosphenotic, three infraorbitals, the lachrymal, the antorbital and the supraorbital. There is

no evidence that the antorbital and supraorbital had any relation with the infraorbital sensory canal.

The supraorbital (So, Figs. 1, 5, 6) is a large, oval bone, overlying the supraorbital flange of the frontal posteriorly and extending antero-ventrally. The anterior half of the bone has a ridge along its centre and is angular in section. The antorbital (Ao, Figs. 1, 5) is a small, comma-shaped bone, with a broad posterior part articulating with the lateral face of the supraorbital, and a slender anterior shaft fitting against the upper edge of the lachrymal.

The lachrymal and infraorbitals are very thin, flimsy bones. The lachrymal (Lac, Figs. 5, 6) is large and roughly triangular, meeting the antorbital above and overlapping the supramaxillae below. The infraorbital sensory canal passed through a tube near the upper edge of the bone, giving off three large branches which open near the ventral edge. The second infraorbital (Io2, Fig. 6) is a slender bone, about

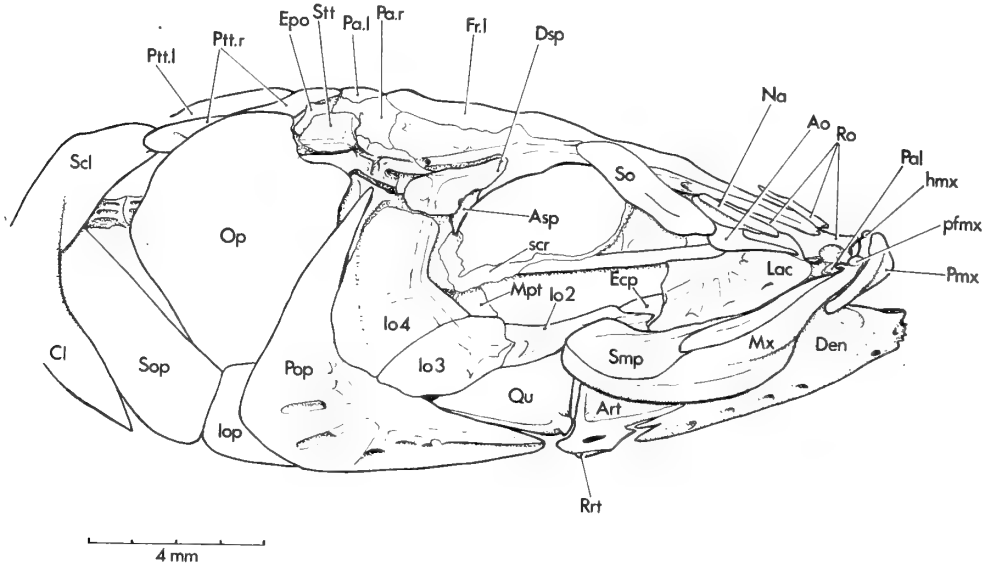

FIG. 6. *Gaudryella gaudryi* (Pictet & Humbert). Skull as preserved in P.48047, Hajula, Lebanon. The suffixes ' r ' and ' l ' denote bones of the right and left side, explanation of other abbreviations p. 296.

equal to the lachrymal in length, with the sensory canal passing through a tube along its centre. There is no evidence of pores or branches of the canal in the second infraorbital, but this is possibly due to deficiencies of preservation. The third infraorbital (Io3, Figs. 5, 6) is short but expanded posteriorly, extending back to the preopercular. The tube for the sensory canal runs some distance from the orbital margin of the bone, and is bent in the middle of the bone, giving off a short branch at this angle. Like the third, the large fourth infraorbital (Io4, Figs. 6, 9) is expanded, reaching the preopercular, and has the tube for the sensory canal some distance from

its orbital margin, with a bend midway down the bone and a branch passing back from this angle. Comparison with *Humbertia* (p. 239) and other primitive teleosts (see illustrations in Nelson 1969b) indicates that the large fourth infraorbital of *Gaudryella* incorporates the fourth and fifth infraorbitals. The presence of a branch and pore midway down the bone is positive evidence that such a fusion has taken place, because pores develop only between neuromasts, showing that the bone must contain two neuromasts, whereas there is only one in each posterior infraorbital of primitive teleosts.

The dermosphenotic (Dsp, Figs. 1, 6) is an elongate, triangular bone overlying the autosphenotic and frontal, covering the dilatator fossa. The dermosphenotic ends well short of the supraorbital, leaving a gap in the circumorbital series. The infraorbital canal ends blindly in the anterior part of the dermosphenotic, a short branch in the centre of the bone leading back to the temporal canal in the pterotic.

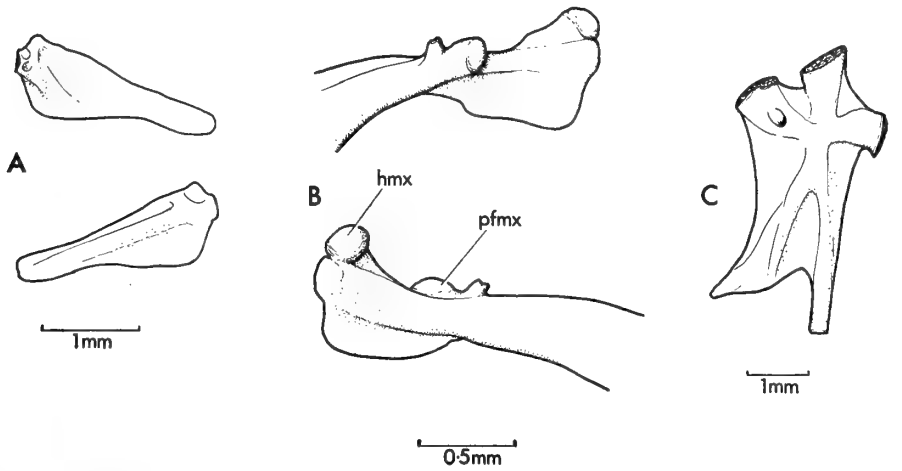

FIG. 7. *Gaudryella gaudryi* (Pictet & Humbert). A, isolated right premaxilla, P.51251, in internal (above) and external view. B, head of isolated right maxilla, P.51252, in external (above) and internal view. C, isolated right hyomandibular, P.51253, in medial view. All from Hajula, Lebanon. Explanation of abbreviations p. 296.

(iv) *Hyopalatine bones.* The hyomandibular (Hm ; Fig. 7C) is vertical or inclined slightly backwards. The head of the bone is divided into two portions, approximately equal in size. The opercular process lies in the upper third of the bone, opposite the foramen for the hyomandibular nerve on the medial surface of the bone. Ventrally the hyomandibular has a broad, membranous process extending antero-ventrally across the metapterygoid.

The metapterygoid (Mpt, Figs. 6, 9) is never clearly visible and seems to have been reduced. It consists of the usual two parts, an outer, ' D '-shaped lamina meeting the quadrate ventrally and covering the outer surface of the shaft of the hyomandibular, and a lamina extending dorso-medially to cover the posterior part of the endopterygoid and meet the antero-ventral process of the hyomandibular.

The symplectic (Sym, Fig. 9) is long and the quadrate (Qu, Figs. 5, 6, 9) is strongly inclined forwards, so that its postero-ventral margin is almost horizontal. The quadrate condyle lies below the centre of the orbit. The ectopterygoid (Ecp, Figs. 5, 9) is a slender, elongate bone, fitting against the anterior edge of the quadrate and curving forwards to meet the palatine. There is no sign of teeth on the ectopterygoid. The endopterygoid is a long, toothless lamina, supported by the palatine, ectopterygoid and metapterygoid, and articulating with the parasphenoid medially. The palatine (Pal, Figs. 5, 9) is straight, rather long, and toothless but heavily ossified. Anteriorly it ends in a large articular head, bearing a medially directed facet which articulates with the vomer and mesethmoid and a larger, laterally directed facet which articulates with a condyle on the upper edge of the maxilla.

(v) *Dermal upper jaw.* The dermal upper jaw consists of the premaxilla, maxilla and two supramaxillae. The premaxilla (Pmx, Figs. 5, 6 ; Fig. 7A) is a curved, toothless slip of bone, about one-quarter as long as the maxilla. An oblique ridge crosses the outer surface of the bone, ending in a rudimentary ascending process which fits against the condylar head of the maxilla, and there is a small internal process on the medial edge of the bone which was probably the site of insertion of the interpremaxillary ligament. There is no articular process.

The maxilla (Mx, Figs. 5, 6, 9) is deep and curved, ending in front of the level of the centre of the orbit. The head of the bone (Fig. 7B) is deep, with the cranial condyle (hmx) placed dorsally and a vertical flange below it which probably met its fellow in the mid-line. The cranial condyle articulated with the mesethmoid, the flange below it with the vomer. The ventral flange extends laterally behind the premaxilla. Lateral to the cranial condyle there is a large, rounded condyle (pfmx) on the dorsal surface of the maxilla which articulated with the head of the palatine (cf. Kirchhoff 1958, fig. 12 ; Gosline, Marshall & Mead 1966 ; Vrba 1968, fig. 3). Immediately behind this palatine condyle there is a postero-dorsally directed process on the maxilla which may have served for the insertion of the palato-maxillary ligament (cf. *Elops*, Vrba 1968 ; *Vinciguerria*, Weitzman 1967b ; and *Clupea*, Kirchhoff 1958), but whose shape is such that it must also have housed the ligament passing back to the lower jaw (cf. Gosline 1969 : 194 ; Weitzman 1967b : 516 ; Vrba 1968, *l. maxillo-mandibulare posterius*). Behind the premaxilla, the maxilla becomes deeper and blade-like. The oral border of this part of the bone is set with minute clustered teeth which extend on to the inner surface of the bone a little. The dorsal edge of the toothed part of the maxilla is shaped to accommodate the supramaxillae.

The anterior supramaxilla (Sma, Figs. 5, 6, 9) is a long, slender strap-like bone, ending just behind the process for the palato-maxillary ligament on the maxilla. The posterior supramaxilla (Smp, Figs. 5, 6, 9) has an ovoid body with a long anterior process extending above the posterior two-thirds of the anterior supramaxilla. The supramaxillae are displaced in specimens fossilised with the mouth open (Figs. 5, 9), showing that they were mobile, as in clupeoids (Kirchoff 1958, fig. 39).

(vi) *Lower jaw.* The mandible (Fig. 8) is deep, with a short oral border and a high, rounded coronoid process. It consists of four bones, dentary, angulo-articular, retroarticular and a small ossification of Meckel's cartilage (sesamoid articular). The dentary (Den, Figs. 6, 8, 9) forms more than four-fifths of the upper and lower

borders of the jaw. The symphysis is moderately deep and has three or four characteristic antero-ventral projections or serrations, presumably for the insertion of symphysial ligaments. Close to the symphysis there is a single row of five or six small, recurved teeth. Behind the teeth, the oral border of the dentary rises sharply into the coronoid process, as in *Leptolepis*, many clupeoids, *Coregonus*, *Hypomesus*, etc. The coronoid process has a concave anterior edge, and is highest anteriorly. At the base of the coronoid process, just behind the tooth row, there is a well marked depression on the outer face of the dentary for the insertion of the ' lip ' ligaments (anterior maxillo-mandibular ligament). On the medial face of the dentary there is a moderately large pocket in which the angulo-articular is inserted.

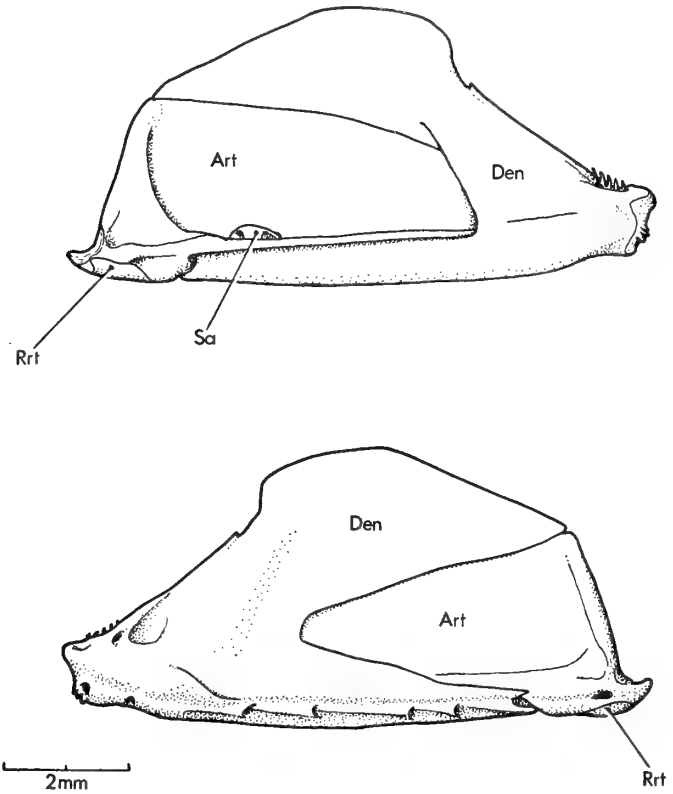

FIG. 8. *Gaudryella gaudryi* (Pictet & Humbert). Isolated left lower jaw in medial (above) and lateral view. P.51254, Hajula, Lebanon. *Sa*, sesamoid articular ; explanation of other abbreviations p. 296.

The dermal and endochondral portions of the angulo-articular (Art, Figs. 6, 8, 9) are indistinguishably fused. The articular surface for the quadrate is not deeply excavated, and there is only a very short retroarticular process. The coronoid process of the angulo-articular rises sharply in front of the articular facet, and the bone

extends forwards as a tapering lamina, fitting into the pocket in the dentary anteriorly. The mandibular sensory canal, passing forwards from the preopercular, entered the retroarticular process of the angulo-articular, passed through the bone with one elongate pore en route, and then traversed the dentary. There is a pore at the suture between the dentary and angulo-articular, and in the dentary there are four postero-ventrally directed branches opening by pores near the ventral edge of the bone, one pore below the anterior edge of the coronoid process, and one pore just behind the projections at the symphysis.

The retroarticular (Rrt, Figs. 6, 8, 9) is a small slip of bone applied to the postero-ventral surface of the angulo-articular. The sesamoid articular (Sa, Fig. 8) is a small half-cylinder of perichondral bone on the medial face of the angulo-articular.

(vii) *Hyoid arch and branchiostegals.* The hyomandibular is described above, with the palate. The interhyal is the usual short, waisted rod. The ceratohyal (Figs. 9, 32) is ossified in two pieces. The proximal ceratohyal (Pch) is an elongate, triangular bone, with a groove for the hyoidean artery near the upper edge of its outer face. The distal ceratohyal (Dch) is rectangular, with a deeply concave lower margin. The groove for the hyoidean artery runs just above the centre of the outer face of the bone, and is interrupted by an elongate, oval fenestra. There are two hypohyals. The lower hypohyal (Hhl, Fig. 9) is a large, square bone, articulating with its fellow by a facet at the antero-ventral corner. The upper hypohyal (Hhu, Fig. 9) is rarely clearly visible, evidently because it was small and inclined medially so that it is usually crushed between the large lower hypohyals. The foramen of the hyoidean artery lies entirely within the upper hypohyal. There is no sign of an ossified basihyal. In front of the hypohyals there is a heart-shaped dermal plate bearing small marginal teeth (Bht, Fig. 9) which was probably underlain by an unossified basihyal. There is a very long, slender urohyal (Uh, Fig. 9) extending from the hypohyals back to the cleithral symphysis. The head of the urohyal is forked and its anterior half is rod-like. The posterior half of the bone bears a pair of broad, ventro-lateral laminae whose anterior margins curve forwards in a characteristic way (Fig. 9).

There are eleven branchiostegals (Brr, Fig. 9 ; Fig. 32), seven inserted on the distal ceratohyal, one on the line of junction between the distal and proximal ceratohyals, and three on the proximal ceratohyal. The first six rays are thin and hair-like, the next three broader and acinaciform (McAllister 1968), the last two spathiform and curved upwards distally.

(viii) *Branchial arches.* Fragments of the gill arch skeleton are visible in several specimens, notably P.13876, but they show nothing remarkable and the pharyngeals are not visible. The first gill arch bore very long, toothless, close-packed gill-rakers, reaching 2.5 mm. in length in a fish of 17 mm. head length.

(ix) *Opercular bones.* The preopercular (Pop, Figs. 6, 9) is expanded at the angle and has the horizontal limb only a little shorter than the vertical limb. The vertical limb ends close below the pterotic and there is no suprapreopercular. The preopercular sensory canal ran in a closed tube lying close to the anterior edge of the bone. One or two small, postero-dorsally directed branches leave this tube above the angle, while at and below the angle there are four or five branches. The upper-

most of these branches has a short intraosseous portion opening into a long groove running postero-ventrally, the next branch has a larger bone-enclosed portion opening into a shorter groove, and the remaining two or three branches open ventrally, close to the main canal. The anterior part of the canal ran in a groove which is open ventrally.

The opercular (Op, Figs. 6, 9) has an excavated antero-dorsal margin and a rounded upper edge, extending up to the post-temporal. The subopercular (Sop, Figs. 6, 9) is moderately large, with the usual spike at its antero-dorsal corner. The upper edge of the subopercular lies at about 65° to the anterior edge of the opercular. The interopercular (Iop, Figs. 6, 9) is a very long triangular bone, largely concealed by the preopercular. Apart from a few shallow, radiating grooves on the opercular, there is no ornament on the opercular bones, and they are not covered by scales.

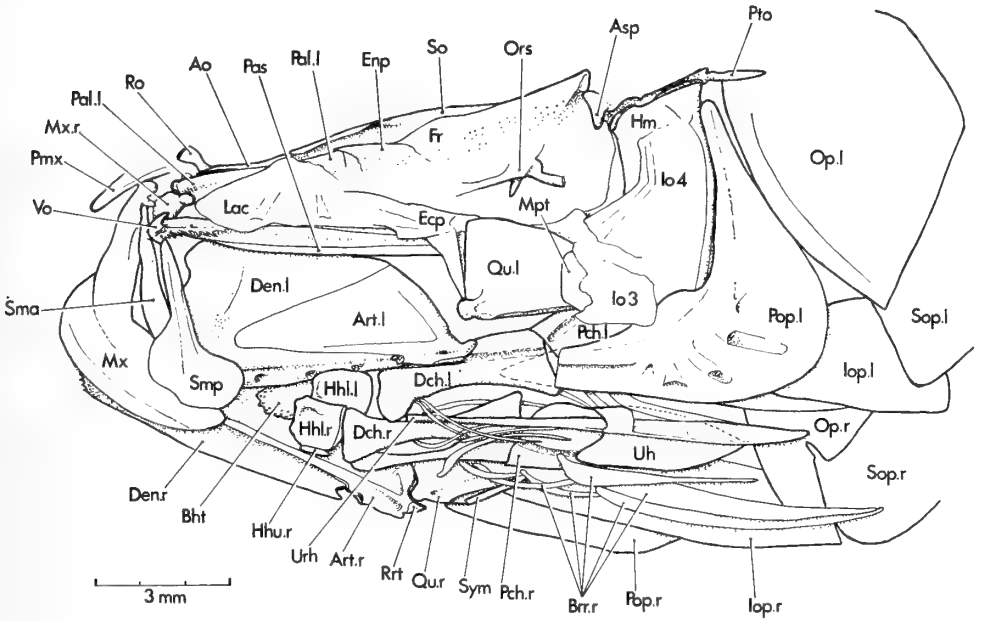

FIG. 9. *Gaudryella gaudryi* (Pictet & Humbert). Skull crushed in ventro-lateral aspect, as preserved in P.9991, Hajula, Lebanon. The suffixes 'r' and 'l' denote bones of the right and left side, explanation of other abbreviations p. 296.

(x) *Vertebral column.* There are 41–44 vertebrae (mean of 13 specimens is 43·0) and a free second ural centrum (Fig. 33). Normally there are fifteen caudal vertebrae (range 13–16) and twenty-eight abdominals. The centra are slightly longer than high, and are well ossified, with longitudinally ridged lateral surfaces but with a narrow, open notochordal canal. The neural and haemal arches of the caudal vertebrae and the neural arches and parapophyses of the posterior abdominal vertebrae are fused to the centra, but on the first twelve to fifteen vertebrae the neural arches and the large, triangular parapophyses are autogenous. The neural arches

and spines are paired structures on the first four or five vertebrae, but are fused in the mid-line on the remaining vertebrae. There are seven or eight rod-like supraneurals above the anterior vertebrae. The epineurals are outgrowths of the neural arches on the first eight to ten vertebrae, but are separate ossifications on succeeding vertebrae. The last epineural is in the region of the last abdominal vertebra. The epineurals are simple rods, with no bifurcation. There are no pleural ribs on the first two vertebrae, but the first centrum has a pair of short, postero-lateral processes, probably for the insertion of Baudelot's ligament. The remaining abdominal vertebrae bear stout pleural ribs extending to the ventral margin of the trunk. The heads of the ribs are expanded antero-ventrally and postero-dorsally, and articulate with similarly elongated facets on the parapophyses. The parapophyses of the last six or seven abdominal vertebrae increase in length progressively while the ribs decrease in size. Rod-like epipleurals articulate with the parapophyses of the abdominal vertebrae and sometimes extend to the first two or three caudal vertebrae. The neural and haemal spines of pre-ural vertebrae 3–7 increase progressively in length and thickness. The caudal skeleton is described below, together with the caudal fin.

(xi) *Pectoral girdle and fin.* The supratemporal (Stt, Fig. 6) is a flimsy, triangular bone which is always more or less crushed into the opening of the post-temporal fossa: the bone overlies the parietal and epiotic medially and covers the opening of the post-temporal fossa laterally. The lateral line canal from the post-temporal entered the supratemporal posteriorly and bifurcated near its anterior margin, a short antero-lateral branch transmitting the temporal canal to the pterotic, and a longer medial branch transmitting the supratemporal commissure to the transverse groove on the parietal.

The post-temporal (Ptt ; Fig. 11A) has a short, stout ventral limb articulating with the intercalar and a long, curved dorsal limb extending antero-medially and almost meeting its fellow in the mid-line above the supraoccipital. Probably the post-temporal was attached to the epiotic by a ligament. The lateral line canal penetrated the bone near its ventral margin, giving off two branches dorsally en route.

The supracleithrum (Scl, Fig. 10) is long and broad, arching forwards from its contact with the lateral face of the cleithrum to articulate with the postero-ventral part of the post-temporal. The lateral line canal from the anterior lateral line scale passed obliquely up through the bone into the post-temporal.

The cleithrum (Cl ; Figs. 10, 11) has a long upper part, above the fin insertion, with a very broad, triangular posterior plate, and a short ventral part, arching forwards to the cleithral symphysis. The medial edge of the central portion of the bone is turned inwards to form the hind margin of the gill chamber, as usual. There are two postcleithra, the upper a rather large, plate-like bone lying medial to the posterior plate of the cleithrum, the lower (Pcv, Fig. 10) a flattened rod passing postero-ventrally from the lower edge of the upper.

The endoskeletal pectoral girdle consists of three bones, scapula, coracoid and mesocoracoid. The scapula (Sca ; Fig. 11B) has a large scapular foramen near its antero-ventral margin, a postero-dorsal process which is applied to the medial face of the cleithrum, and the usual saddle-shaped facet for the first pectoral fin-ray. The coracoid (Cor, Fig. 10) is rather large, with a deep anterior process passing forwards to

the tip of the cleithrum, leaving a triangular fenestra between this contact and the upper attachment of the coracoid to the cleithrum. A short antero-dorsal process of the coracoid joins with a similar process of the scapula in receiving the ventral end of the mesocoracoid. Just below this process on the medial face of the coracoid

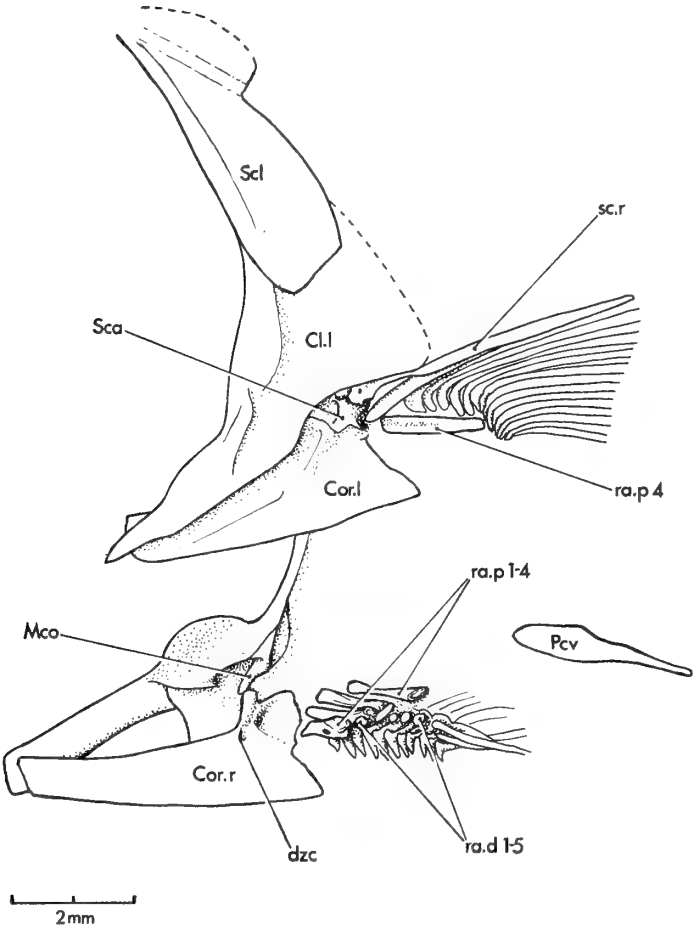

FIG. 10. *Gaudryella gaudryi* (Pictet & Humbert). Pectoral girdle as preserved in P.9991, Hajula, Lebanon. Above is the left girdle in lateral view, below the right girdle in medial view. *dzc*, diazonal canal in coracoid ; *Mco*, mesocoracoid; *Pcv*, ventral postcleithrum ; *ra.d* 1–5, distal pectoral radials ; *ra.p* 1–4, proximal pectoral radials ; *sc.r*, scale-like upper hemitrich of first pectoral ray ; suffixes ' r ' and ' l ', bones of right and left side ; other abbreviations p. 296.

there is a diazonal canal (dzc, Fig. 10) leading antero-ventrally. The mesocoracoid (Mco, Fig. 10) is an arched strut extending down from its expanded attachment to the cleithrum to meet the scapula and coracoid.

There are four proximal pectoral radials (ra. p. 1–4, Fig. 10). The uppermost is short, of complex form, and pierced by a canal. The lower three radials increase progressively in length and take the form of compressed rods, broader at each end. There is a series of distal pectoral radials, small, nodular ossifications lying between the bases of the hemitrichs of the upper fin-rays. P.9991 shows five distal radials (ra. d 1–5, Fig. 10), while in P.48048 and AM 3783 there appear to be at least six.

The pectoral fin contains fifteen or sixteen rays (more commonly 16), all segmented distally. The longest rays of the fin, the third and fourth, are equal in length to eight vertebrae. The first ray, which articulates directly with the scapula, is very asymmetrical, with its upper hemitrich modified into a thin, scale-like plate (sc.r, Fig. 10), segmented distally.

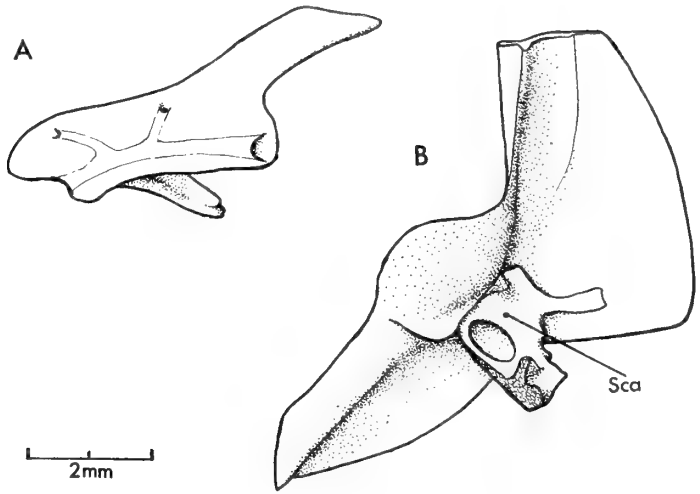

FIG. 11. *Gaudryella gaudryi* (Pictet & Humbert). A, isolated right post-temporal, P.51255, in lateral view. B, ventral part of isolated right cleithrum and scapula, P.51256, in medial view. From different individuals, Hajula, Lebanon.

(xii) *Pelvic girdle and fin.* The pelvic girdle lies below the middle part of the dorsal fin and the pelvic fins originate below the last rays of the dorsal, at about the twenty-first vertebrae. Each pelvic bone (Fig. 12) consists of an antero-medially inclined shaft of thin, membranous bone, and a medial process of thicker, endochondral bone, both these portions meeting their antimeres in the mid-line. The pelvic bone has a complex articular surface at its postero-lateral corner. Above this surface there is a curved, postero-lateral process of dense bone, arising on the dorsal surface of the pelvic bone and projecting alongside the base of the upper hemitrich of the first pelvic ray (p. sp, Fig. 12) : this process appears to represent the pelvic splint, here fused with the pelvic bone. Only a single ossified pelvic radial has been seen (p.ra, Fig. 12C), projecting posteriorly medial to the base of the innermost fin-ray (cf. Gosline, Marshall & Mead 1966, fig. 3 ; Weitzman 1967b, figs. 5, 6, 16). Other pelvic radials may be present, obscured by the bases of the fin-rays.

The pelvic fin contains 12 (3 of 8 specimens) or 13 (5 of 8 specimens) rays, all segmented distally. As noted above, the short, hooked splint is fused with the pelvic girdle. The pelvic fin is shorter than the pectoral, the longest rays being equal in length to about five vertebrae.

(xiii) *Dorsal and anal fins.* The dorsal fin (Fig. 33) lies at the mid-point of the back of the fish and occupies a length of about six vertebrae. The fin contains twelve rays supported by eleven radials. A twelfth radial is present, but carries no fin-ray, only a posterior expansion of the head. The first radial has a stout anterior process from its head. Except for the first three or four, the radials have separate ossified middle segments. The shaft of the first radial ends above the thirteenth or fourteenth vertebra. The dorsal fin-rays are all segmented distally and all except the first two are branched. The longest fin-ray, the third, is equal in length to about eight vertebrae, a little less than the maximum depth of the trunk.

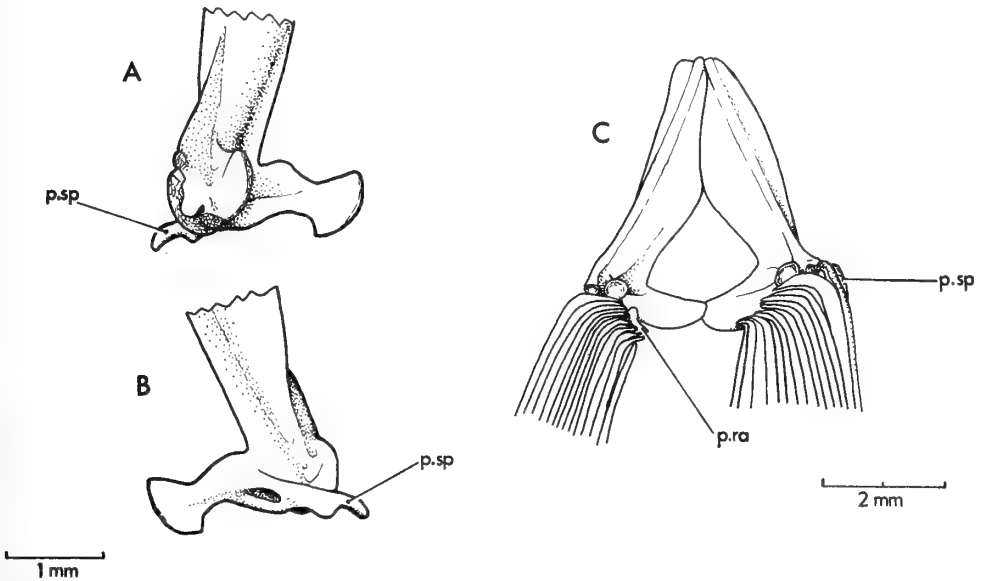

FIG. 12. *Gaudryella gaudryi* (Pictet & Humbert). A,B, posterior part of isolated right pelvic bone, P.51257, in ventral (A) and dorsal (B) view. C, pelvic girdle and fins in ventral view, as preserved in P.9991. Both from Hajula, Lebanon. *p.ra*, inner pelvic radial ; *p.sp*, pelvic splint.

The anal (Fig. 33) is small and remote, originating below the tenth pre-ural vertebra and occupying a length of four vertebrae. The fin contains nine rays supported by eight radials. The fin-rays are slender and short, the longest being about equal to the base length of the fin. All are segmented distally and all but the first two are branched. The first radial ends proximally close to the haemal spine of the third caudal vertebra.

(xiv) *Caudal skeleton and fin.* The caudal skeleton (Figs. 13, 14) is considerably specialised by fusion of parts. The neural and haemal spines of the third and fourth pre-ural vertebrae are long and slightly expanded distally : the haemal spine of PU3 is autogenous and has a small anterior lamella near the base. The neural spine of PU3 also has a small anterior lamella (Fig. 14). In some specimens the foremost procurrent caudal rays articulate with the neural spine of PU3 above and the haemal spine of PU4 below, in others they articulate with the first epural above and the haemal spine of PU3 below. PU2 has a leaf-like neural spine (npu2), about half as long as its predecessor, as in *Elops*, *Aulopus* and *Nematonotus* (Patterson 1968b : 84), and a long, stout haemal spine with anterior and posterior lamellar expansions, the anterior one touching the preceding haemal spine proximally, the posterior one fitting against a similar expansion from the parhypural. The haemal arch of PU2

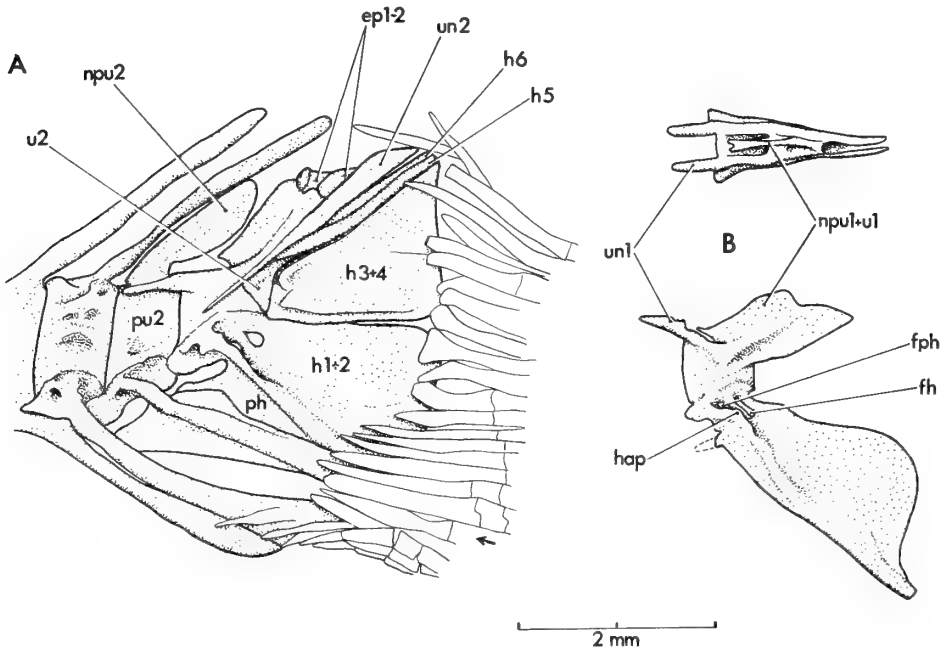

FIG. 13. *Gaudryella gaudryi* (Pictet & Humbert). A, caudal skeleton as preserved in P.9991 ; an arrow marks the lowermost (unbranched) principal fin-ray. B, isolated compound centrum and attached structures, P.51258, in dorsal (above) and left lateral view. Both from Hajula, Lebanon. Explanation of abbreviations p. 296.

is certainly autogenous, the neural spine is probably also autogenous, but the suture between arch and centrum is always covered by the first uroneural. The first preural and ural centra are fused and form part of a complex structure (Fig. 13B) into which are also fused the parhypural (ph), the two lower hypurals (h1+2) and the stegural. A line of fusion is often visible between the compound centrum and the combined parhypural and lower hypurals : evidently this fusion occurred during

ontogeny. Similarly, there may be a line of fusion between the parhypural and the first hypural, but the first and second hypurals are indistinguishably fused, only the hypural foramen (fh, Fig. 13B : Monod 1968 : 640) indicating that the second hypural is incorporated. The parhypural has a rudimentary hypurapophysis (hap), and is a little longer than the first hypural but much more slender. The stegurals have paired ventral parts, representing the first uroneural (un1), extending forwards and back from the compound centrum, and a median dorsal crest arching forwards over the narrow neural canal and fitting against the second pre-ural neural spine, presumably representing the neural arches of the first ural and pre-ural centra (npu1 + u1).

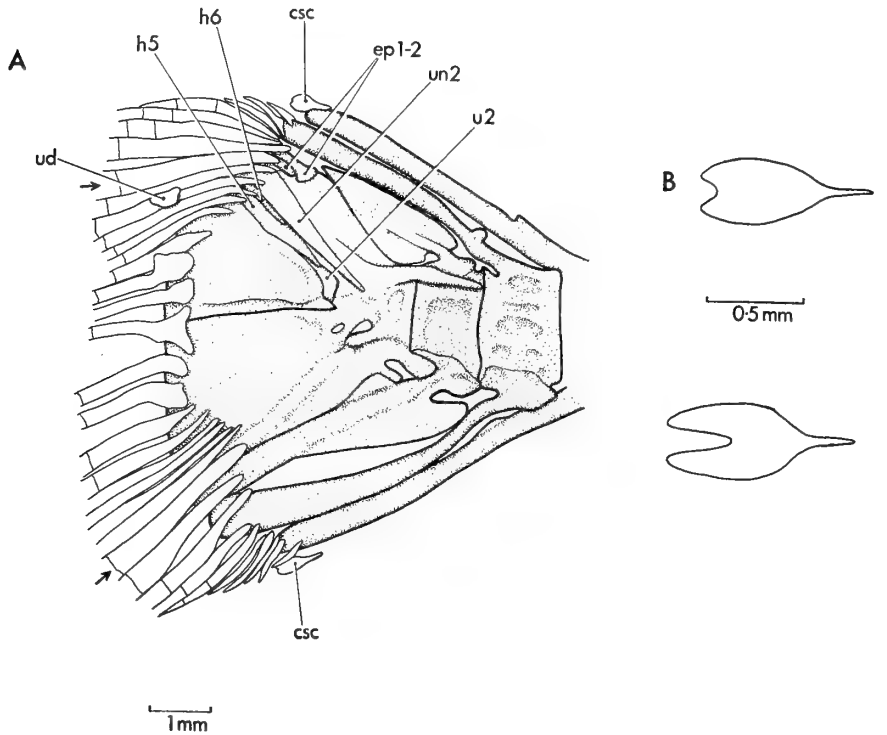

FIG. 14. *Gaudryella gaudryi* (Pictet & Humbert). A, caudal skeleton as preserved in AM 5579 ; arrows mark the outermost (unbranched) principal fin-rays. B, upper (above) and lower caudal scutes, restored on the basis of AM 5568. Both from Hajula, Lebanon. Explanation of abbreviations p. 296.

The first uroneural was evidently forked proximally (cf. *Humbertia*, Figs. 26, 27) as in *Elops* and *Nematonotus*, and is therefore probably compound in origin (Patterson 1968a : 226). The upper fork extends forwards across the second pre-ural centrum while the ventral fork is fused into the compound centrum. Posteriorly the stegurals extend back as a broad, paired flange, with a lateral groove housing the second

uroneural. The second uroneural (un2) is slender and pointed anteriorly, where it fits in the groove on the stegural, and broad posteriorly. There is no third uroneural.

There is a small independent second ural centrum (u2), supporting the upper hypurals. There appear to be four upper hypurals, the third and fourth (h3+4) very broad and fused together, but often with a partial suture suggesting that fusion occurred during ontogeny, the fifth and sixth (h5, h6) very slender and separate. The fifth and sixth hypurals sometimes give the impression of uroneurals, since their proximal ends extend forwards alongside the second uroneural in slender points, that of the fifth hypural lying dorso-lateral to the second ural centrum, as in *Esox* (Monod 1968 : 355), *Humbertia* (p. 248), *Argentina* (Fig. 38) and osmerids (Fig. 43). There are two epurals (ep 1–2) above the posterior part of the stegural. The first epural is broad and expanded proximally, the second is slender.

The forked caudal fin contains nineteen principal rays with seventeen branched (nine in the upper lobe, eight in the lower). There are five to seven upper procurrent rays, the first two or three unsegmented, and seven to nine lower procurrent rays, the first two to four unsegmented. Close to the foremost procurrent fin-ray above and below there is a very small, leaf-shaped caudal scute (csc ; Fig. 14B). There is a single urodermal (ud, Fig. 14A), lying on the second fin-ray below the uppermost principal ray, well clear of the uroneurals.

(xv) *Squamation.* The scales are very thin and are always poorly preserved. They are cycloid, with continuous, well separated circuli, and contain no bone-cell spaces. The scales are large, the lateral line scales being equal in depth to almost a quarter of the depth of the trunk, and there can only have been six to eight scales in a transverse series on the trunk. There is a broad, continuous lateral line, the number of lateral line scales being approximately equal to the number of vertebrae. There are no scales on the cheek or operculum, or on the bases of the fins.

(xvi) *Soft anatomy.* In most of the specimens from Hajula the musculature is preserved as a cream coloured phosphatic mass. Myocommata are occasionally visible within this mass. The course of the gut is indicated by its fossilised contents, showing that the anus lay close in front of the origin of the anal fin, below the third or fourth caudal vertebra.

There is no convincing evidence of an adipose fin, despite attempts to discover one by various stains, ultraviolet light, etc. But even in the myctophoids from these deposits, which surely had adipose fins and which are usually preserved in lateral view, the fin is never clearly demonstrable.

In some specimens the pigment of the retina is preserved, indicating that the eye was large, filling the orbit and having a diameter about equal to one-third of the braincase length. The same specimens show the pattern of chromatophores on the trunk, demonstrating that the back was uniformly pigmented and the belly was white.

As noted above, the scales consist of acellular bone, and this is true of the rest of the skeleton, dermal and endochondral, except for certain areas, mostly close to articular surfaces, where the bone is densely cellular, containing small, rounded chondrocyte-like spaces, without canaliculi. These cellular areas include the cranial condyle and palatine facet of the maxilla, the head of the vomer and palatine, the

antero-dorsal corner of the coronoid process of the dentary, the condyle of the quadrate, the antero-ventral corner of the lower hypohyal and the glenoid region of the scapula and coracoid.

Humbertia gen. nov.

DIAGNOSIS. Small, slender, round-bodied salmoniform fishes ; parietals in contact medially and bearing the supratemporal commissure, post-temporal fossa roofed ; nasals long and tubular ; rostral not distinct from mesethmoid, which is flat and shield-like anteriorly with paired splints passing back below the frontals ; vomer broad, toothless, with a long posterior process, parasphenoid toothless, with a rudimentary basipterygoid process ; occipital condyle formed by basioccipital only, intercalar small, wall of otolith chamber somewhat inflated, basisphenoid and orbitosphenoid present, sclerotic ossified ; dermosphenotic and supraorbital large, circumorbital ring of bones almost complete, antorbital, lachrymal and four infraorbitals present, posterior infraorbitals extending to preopercular ; hyomandibular vertical, single-headed, metapterygoid not reduced, quadrate condyle below centre of orbit, no pterygoid teeth, a single row of small palatine teeth ; gape small, premaxilla about 40% as long as maxilla, toothed and with rudimentary ascending and articular processes, maxilla toothed, not extending to middle of orbit, two mobile supramaxillae ; mandible with long, high coronoid process, dentary with short, steeply ascending oral border bearing a few small teeth near the symphysis followed by a short diastema and a series of blade-like, serrated teeth, pocket for Meckel's cartilage on inner face of dentary minute ; distal ceratohyal perforate, distal and proximal ceratohyals sutured together, basihyal very small or unossified, toothless ; seven or eight branchiostegals, the posterior ones spathiform and crescentic ; toothless dermal plates fused with second and third basibranchials, upper and lower pharyngeal teeth conical, third hypobranchial long, fourth epibranchial deep and perforated by an efferent arterial foramen, short, toothless gill-rakers on gill arches ; no supra-preopercular, subopercular about as large as opercular ; about 38 vertebrae, 15 caudal, anterior neural arches and parapophyses autogenous, simple epineurals and epipleurals on abdominal vertebrae, anterior epineurals fused to neural arches ; mesocoracoid, two postcleithra and several distal pectoral radials present ; pelvics inserted below posterior part of dorsal, 12–13 rayed, pelvic splint present ; dorsal fin short, lying just in front of mid-point of trunk, anal fin small and remote ; PU2 with short, leaf-like neural spine, lamellar expansions on neural spines of PU3–5 and haemal spines of PU2–3 ; PU1 and U1 fused, U2 separate, six autogenous hypurals ; stegural autogenous and forked proximally, second and third uroneurals present, third lying lateral to second ; three epurals ; caudal fin forked, 19-rayed, one urodermal and large caudal scutes present ; scales large, cycloid, not extending on to skull or fins, lateral line complete ; skeleton mainly acellular.

TYPE (and only) SPECIES. *Humbertia operta* sp. nov.

Humbertia operta gen. et sp. nov.

Pl. 1, fig. 3 ; Pl. 2, fig. 2 ; Pl. 3, fig. 1 ; Pl. 4, fig. 2 ; Pl. 5 ; Figs, 15–27, 30–33

Diagnosis. *Humbertia* reaching about 115 mm. in standard length ; mean proportions (as % standard length) : total length 119, head length 30·5, trunk depth 19·5, predorsal length 41·5, preanal length 82, prepelvic length 56 ; 36–39 vertebrae, mean 38, 15 caudal ; D iii, 11 ; A ii, 6 ; P 16–17 ; V 12–13 ; C v–viii, I, 9, 8, I, v–viii ; eight scales in a transverse series on the trunk, about 40 along the lateral line.

Holotype. BM(NH) P.48218/9 (Pl. 3, fig. 1 ; Fig. 26), a fish in counterpart from Hakel, the part a transfer preparation.

Horizon and localities. Middle Cenomanian, Hakel and Hajula, Lebanon.

Material. The holotype and P.51259 from Hakel, and numerous specimens from Hajula in the BM(NH) and the American Museum of Natural History, especially the following transfer preparations : P.51243, P.51260 (Pl. 4, fig. 2), P.51261–2, P.51263 (Fig. 20), AM 3783 (Figs. 17B, 18), AM 4115 (Pl. 5, fig. 1 ; Fig. 25), AM 4411 (Pl. 5, fig. 2 ; Fig. 19), AM 4580 (Fig. 15A), AM 4590 (Pl. 2, fig. 2 ; Fig. 21), AM 5563 (Fig. 15B), AM 5564 (Fig. 27), AM 5565, AM 5567, AM 5571, AM 5574 (Fig. 15C), AM 5579 ; and the following isolated bones or parts of the skeleton : P.51264 (Fig. 16), P.51265–6 (Fig. 17), P.51267–9 (Fig. 22), P.51270–2 (Fig. 23), P.51273 (Fig. 24).

Description. (i) *General features.* *Humbertia operta* is similar to *Gaudryella gaudryi* in general appearance and it is often very difficult to differentiate the two in unprepared material (Pl. 3). The largest individual, AM 4580, is incomplete posteriorly but must have been about 115 mm. in standard length, almost 30% longer than the largest *Gaudryella* (90 mm.). But, as in *Gaudryella*, such large specimens are unusual and the modal standard length is 60–70 mm. The fish must have been uncompressed, even slightly depressed, since only very occasional specimens are preserved in lateral view (two out of about 50) while dorso-ventral preservation of the head is not uncommon, and the trunk of dorso-ventrally crushed specimens appears broader than in those laterally crushed. The dimensions of nine specimens are given in Table 2 : as in *Gaudryella* the variability in some of these proportions is mainly due to inaccuracies caused by twisting and distortion of the fishes during fossilisation. In comparison with *Gaudryella gaudryi* (Table 1) the caudal fin and head are slightly longer while the predorsal, preanal and prepelvic lengths are slightly smaller, but these differences between the means fall well within the range of variation of the two sets of specimens. The apparent greater depth of the trunk in *H. operta* is perhaps due only to overestimation of the depth of the trunk in most of the listed specimens (only AM 3808 and P.9147 are laterally crushed). Table 2 suggests that in *Humbertia* there was a small relative decrease in head length and prepelvic length with increasing standard length, although this is partially due to the influence of the very small P.51274, a rather distorted fish.

(ii) *Skull roof and braincase.* The skull roof is partially shown in Figs. 15, 19 and is restored in Fig. 30. It differs from that of *Gaudryella* in having a shorter, broader, postorbital division and shorter, broader snout. As in *Gaudryella*, the skull roof is flat apart from the raised tubes containing the sensory canals, but in larger specimens

there are a few ridges radiating from the centre of ossification of the frontal and supraorbital. The supraoccipital (Soc) and epiotics (Epo) are very like those of *Gaudryella*. The parietals (Pa) are always rather poorly preserved. They are shorter and broader than in *Gaudryella*, but as in the latter they are in contact medially, meet the pterotics laterally, roofing the post-temporal fossa, and join the epiotics in digitate sutures postero-laterally. The transverse groove across the parietal which contained the supratemporal commissure is longer, more deeply incised and closer to the posterior edge of the bone than in *Gaudryella*, and shows no sign of division into two parts.

TABLE 2

Proportional measurements of nine specimens of *Humbertia operta*

Specimen	Standard length, mm.	as % standard length: Total length	Head length	Trunk depth	Predorsal length	Preanal length	Prepelvic length
P.51274 (Hajula)	23	118	35	15	41	78	59
P.51275 (Hajula)	51	120	30	20	41	82	57
P.51260 (Hajula)	51	118	31	20	41	82	56
AM 4411 (Hajula)	59	119	31	25	40	80	54
AM 4414 (Hajula)	60	118	32	20	42	84	61
AM 3808 (Hajula)	64	119	33	17	45	86	58
P.9147 (Hajula)	71	118	29	18·5	44	83	53
P.48218 (Hakel)	87	122	27·5	21	41·5	81	52
AM 5570 (Hajula)	110	—	26	18	39	84	52
Mean	—	119	30·5	19·5	41·5	82	56

The frontals (Fr) differ from those of *Gaudryella* principally in having the parietal branch of the supraorbital sensory canal longer and broader, the epiphyseal branch shorter and more posteriorly directed, and in having laminar anterior ends which extend forward to the tip of the snout, dorsal to the mesethoid. The nasals (Na, Figs. 15, 19) are slender and laterally placed, as in *Gaudryella*, but are tubular and much longer than in the latter.

The mesethmoid (Mes, Figs. 15, 19 ; Fig. 16) is very different from that of *Gaudryella*. There is no separate rostral, this dermal element apparently having fused completely with the underlying endo- and perichondral ossification to produce a compound mesethmoid. The dorsal part of the bone is dense and probably mainly dermal in origin. Its upper surface is almost flat, with a broad, shield-shaped anterior part

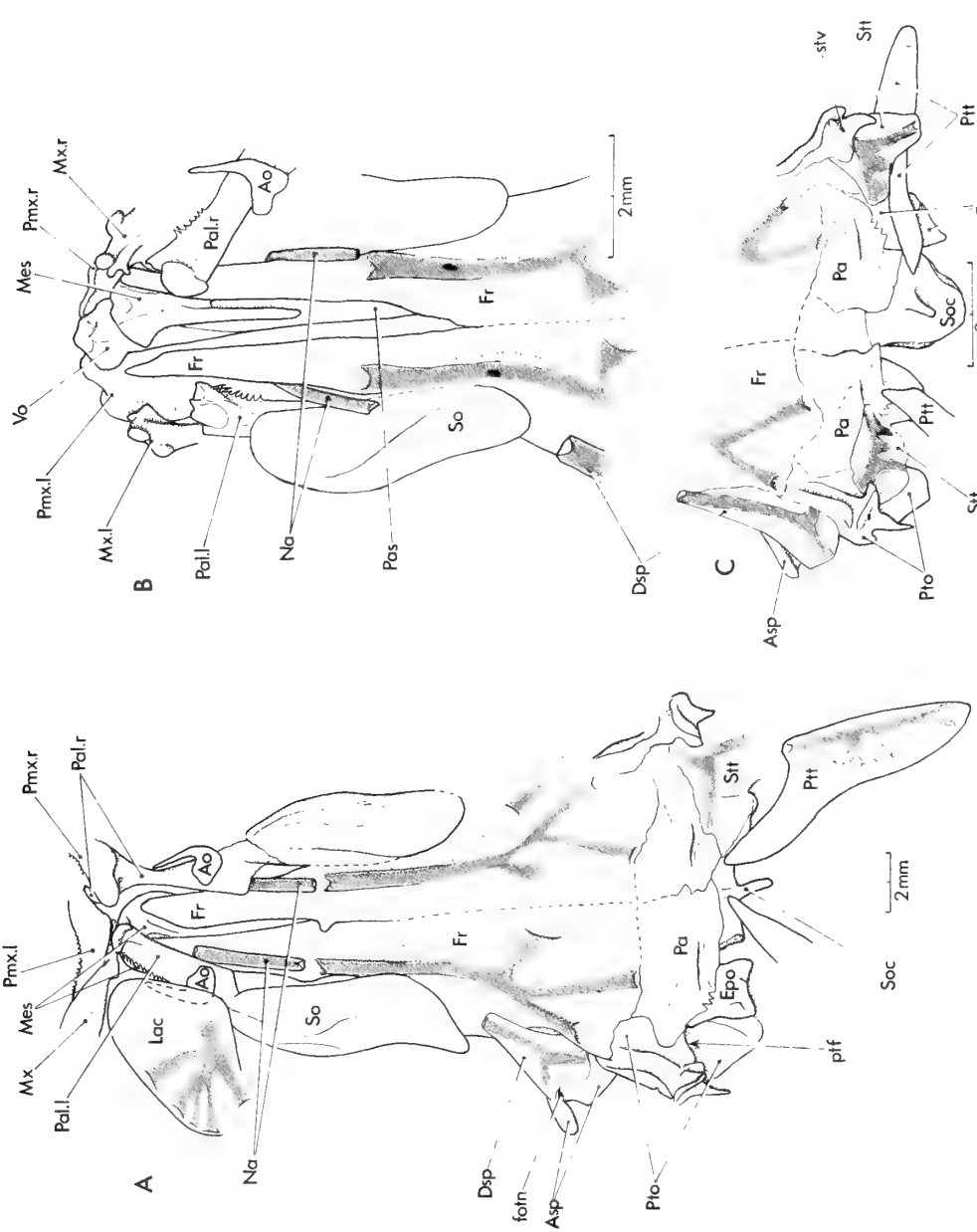

FIG. 15. *Humbertia operta* gen. & sp. nov. A, skull roof as preserved in AM 4580. B, snout as preserved in AM 5583. C, posterior part of skull roof as preserved in AM 5574. All from Hajula, Lebanon. The suffixes 'r' and 'l' denote bones of the right and left side, explanation of other abbreviations p. 296.

and a narrower posterior part ending in a pair of delicate splints which extend back beneath the frontals. At the front of the dorsal surface of the mesethmoid there is a median depression which probably housed ligaments to the ascending processes of the premaxillae. On the underside of the bone there is a pair of vertical laminae of perichondral bone (equivalent to the capsular ethmoids of Weitzman) which splay out anteriorly and end at the widest part of the bone. In front of this point, below the broad anterior part of the bone, there are only traces of granular endochondral bone, and the foremost part of the ethmoid cartilage was apparently unossified. The vertical laminae of perichondral bone are joined ventrally by a horizontal lamina, equivalent to the ventral ethmoid of Weitzman.

The lateral ethmoids (Le, Fig. 21) are quite heavily ossified but are normally hidden below the large supraorbital.

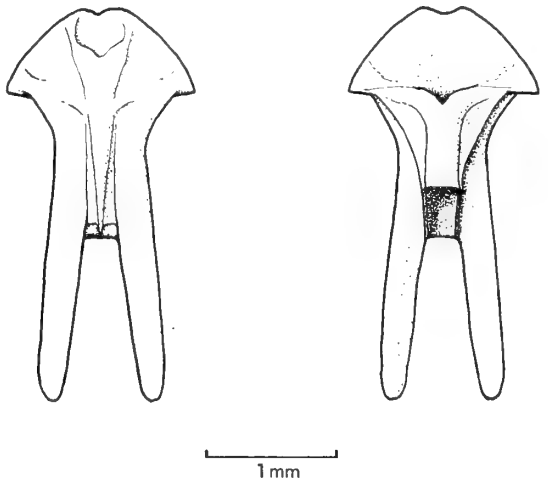

FIG. 16. *Humbertia operta* gen. & sp. nov. Isolated mesethmoid in dorsal (left) and ventral view. Restoration based on P.51264, Hajula, Lebanon.

The vomer (Vo, Figs. 15B, 19 : Fig. 17A) has a broad, rounded head and a long, tapering posterior process extending back below the parasphenoid to the level of the centre of the orbit. The bone is toothless, the underside of its head bearing only a median depression and a pair of lateral depressions into which the palatines fit. On the dorsal surface of the head of the vomer there is a pair of antero-laterally directed facets with which the maxillary heads articulate, and a median knob presenting a pair of articular surfaces for the heads of the premaxillae. The parasphenoid (Pas ; Fig. 17B) is toothless, as in *Gaudryella*. At the hind edge of the orbit the parasphenoid broadens abruptly into a pair of short lateral processes (bpt) which are penetrated by the foramen of the efferent pseudobranchial artery (epsa). These processes appear to be rudimentary basipterygoid processes, homologous with those of osteoglossoids, ichthyodectids (Bardack 1965), the clupeoid *Diplomystus* (Patterson 1967b) and more primitive actinopterygians. Whether in *Humbertia* the

basipterygoid processes articulated with the palate is not possible to discover, but in skulls preserved in lateral view (Fig. 19) the metapterygoid lies very close to the basipterygoid process and such an articulation is likely. Between the bases of the basipterygoid processes there is a very small bucco-hypophysial canal (bhc), patent in the single specimen where both sides of the parasphenoid are visible. The ascending processes of the parasphenoid are long and high, forming the lower part of the somewhat inflated otolith chambers. The ascending process is penetrated by the internal carotid in the usual way (fica). Posteriorly the parasphenoid ends just in front of the occipital condyle (Fig. 18). Probably the myodome opened posteriorly, as in *Gaudryella*.

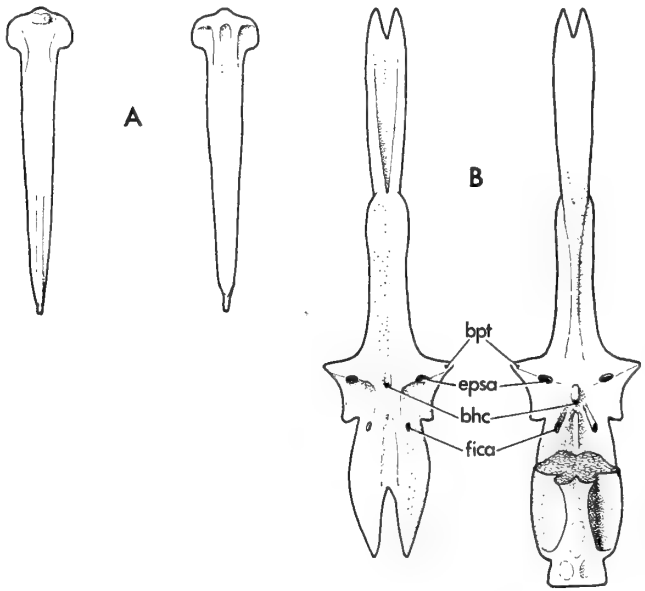

FIG. 17. *Humbertia operta* gen. & sp. nov. A, isolated vomer, P.51265, in dorsal (left) and ventral view. B, parasphenoid in ventral view (left) and in dorsal view with basioccipital in position (right), restorations based on P.51266 and AM 3783. All from Hajula, Lebanon. *bhc*, bucco-hypophysial canal ; explanation of other abbreviations p. 296.

The endocranium is partially visible in several transfer preparations, and parts of the otic and occipital regions are preserved in two dissociated individuals on AM 3783 (Fig. 18). In comparison with *Gaudryella* the endocranium is rather poorly ossified, with cartilagenous interspaces between many of the bones so that they become more or less disarticulated during fossilisation : this break-up of the underlying endocranium is responsible for the poor preservation of the posterior part of the skull roof in this species. As in *Gaudryella*, the occipital condyle is formed by the basioccipital (Boc) alone. The wall of the saccular recess is more inflated than in *Gaudryella* but there is no fenestra at the junction of the prootic (Pro), exoccipital (Exo) and basioccipital. There is some indication of a shallow sub-temporal fossa in the single

specimen showing part of this region, but the intercalar (Ic) appears to be small, with no anterior extension towards the fossa, though again the intercalar is only visible in one specimen and may be incomplete. As in *Gaudryella*, there is no evidence of any association between the ear and the swimbladder. The trigemino-facialis chamber has a lateral opening for the hyomandibular nerve (VII hm) and a rather long jugular canal leading back and opening near the hind edge of the prootic (ptfc). A basisphenoid is present, with a stout pedicel extending down to the parasphenoid.

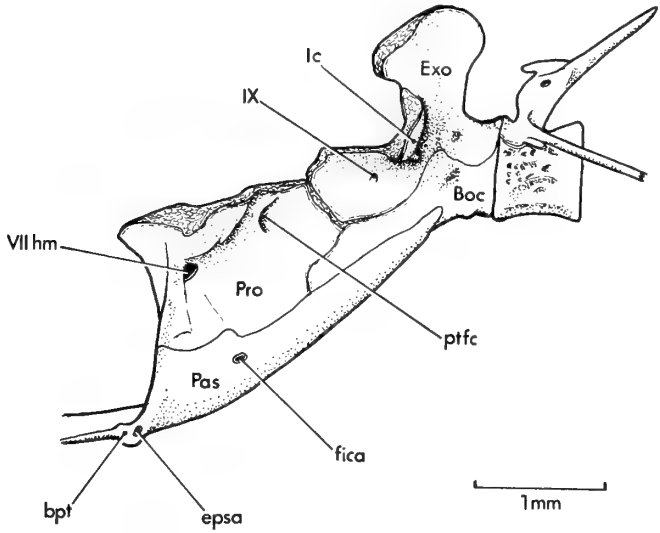

FIG. 18. *Humbertia operta* gen. & sp. nov. Postero-ventral part of neurocranium and first vertebra in left lateral view, restoration based on AM 3783, Hajula, Lebanon. Explanation of abbreviations p. 296.

The hyomandibular facet is single, but is much constricted at the sphenotic/pterotic junction, with expanded, cup-like anterior and posterior regions. The autosphenotic (Asp, Figs. 15, 19, 21) has a spine-like postorbital process forming the anterior margin of a rather deep dilatator fossa. The otic nerve emerged in the upper part of the dilatator fossa, through the base of the postorbital process (fotn). The dermal and endochondral pterotic ossifications are fused into a compound pterotic, as in *Gaudryella*. The pterotic (Pto, Figs. 15A, C, 19) is shorter than that of *Gaudryella* but is similar to the latter in most respects, with the same posterior splint, foramen for the supratemporal branch of the vagus (stv, Fig. 15C), deep groove for the exit of the preopercular sensory canal, and open groove carrying the transverse and longitudinal limbs of the temporal sensory canal. But whereas in *Gaudryella* the groove for the sensory canal is formed only by folding inwards of its outer margin (Fig. 3C), in *Humbertia* the inner edge of the groove projects dorso-medially, especially posteriorly, where it forms a pointed process receiving the sensory canal from the supratemporal.

The pterosphenoids (Pts, Fig. 20) are separated by the optic fenestra and there is a large orbitosphenoid (Ors, Fig. 20), closing the fenestra anteriorly, which differs from the orbitosphenoid of *Gaudryella* in lacking a ventral process in front of the fenestra. The sclerotic is ossified (scr, Fig. 19), probably in four pieces.

(iii) *Circumorbital bones.* There are eight circumorbital bones ; dermosphenotic, four infraorbitals, lachrymal, antorbital and supraorbital (Fig. 31). As in *Gaudryella* there is no sign of any association between the infraorbital sensory canal and the antorbital or supraorbital.

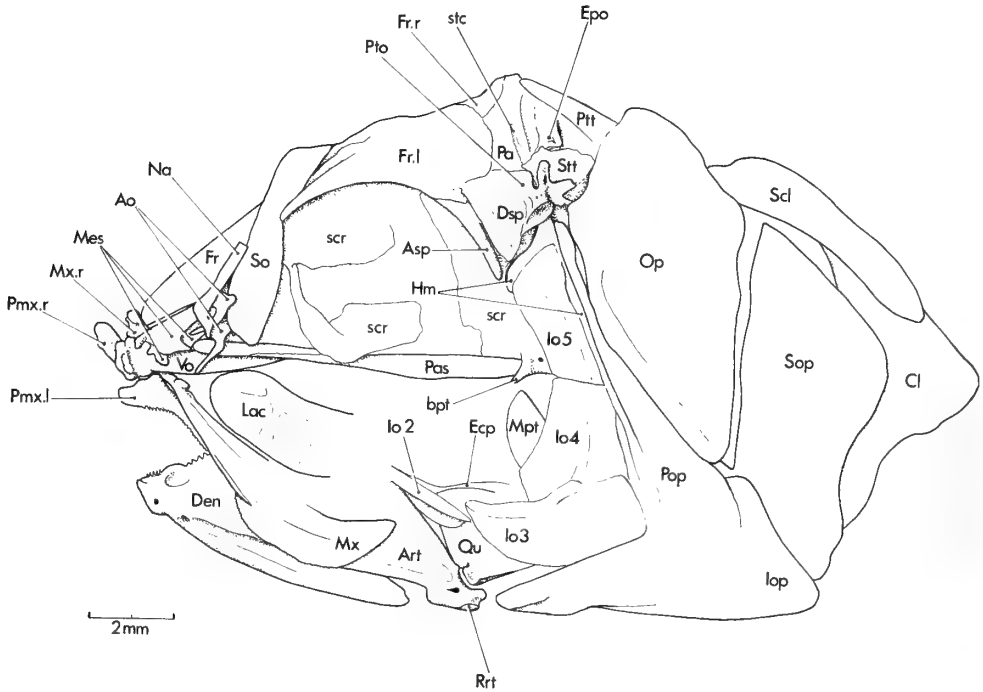

FIG. 19. *Humbertia operta* gen. & sp. nov. Skull as preserved in AM 4411, Hajula, Lebanon. The ventral part of the preopercular, the supramaxillae and the lachrymal and second infraorbital are damaged in this specimen. The suffixes ' r ' and ' l ' denote bones of the right and left side, explanation of other abbreviations p. 296.

The supraorbital (So, Figs. 15, 19) is longer and broader than that of *Gaudryella* but is otherwise similar. Posteriorly the supraorbital ends close to the tip of the dermosphenotic so that the circumorbital ring of bones is almost complete. The comma-shaped antorbital (Ao, Figs. 15, 19) is very like that of *Gaudryella* but is a little deeper posteriorly.

As in *Gaudryella*, the infraorbitals are flimsy bones and are never well preserved. The lachrymal (Lac, Figs. 15A, 19–21) is similar in shape to that of *Gaudryella* but is a little deeper, and has only two ventral branches of the sensory canal which are

broader, end closer to the ventral edge of the bone than the three in *Gaudryella*, and are more frequently bifurcated. As in *Gaudryella*, the second infraorbital (Io2, Figs. 19, 21) is slender and about equal to the lachrymal in length. The sensory canal ran near the centre of the bone in a deep groove which is covered over to form a tube for a short distance in the posterior half of the bone. Behind the eye, where there are only two infraorbitals in *Gaudryella*, there are three in *Humbertia*, as in most primitive teleosts. The third infraorbital (Io3, Figs. 19, 20) resembles that of

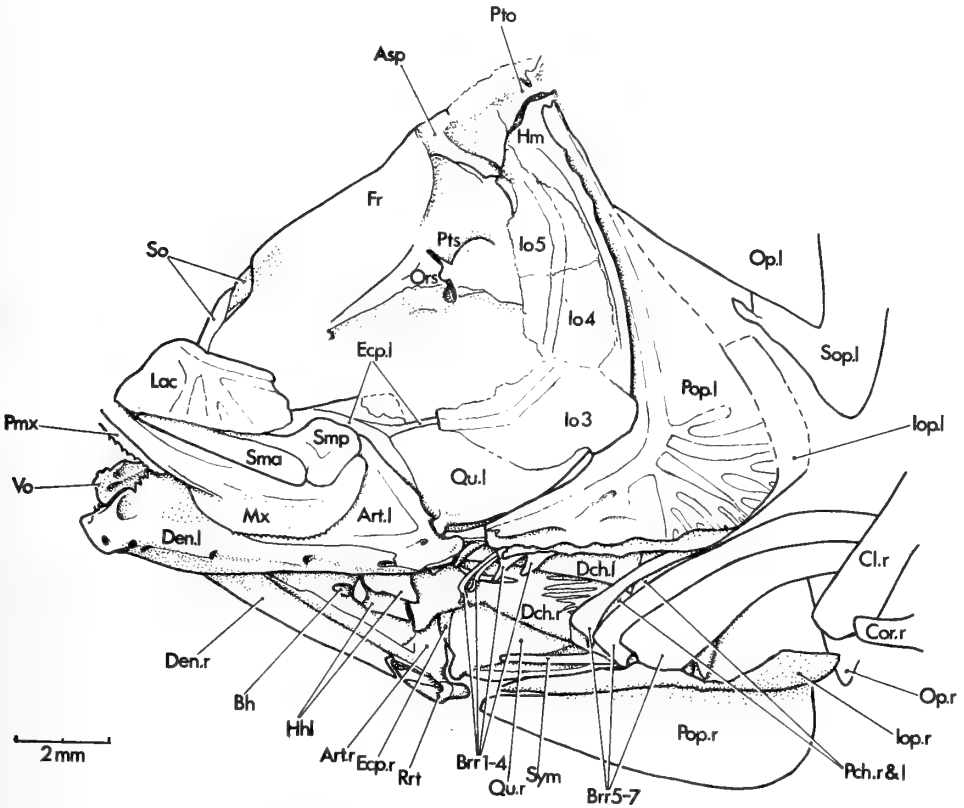

FIG. 20. *Humbertia operta* gen. & sp. nov. Skull crushed in ventro-lateral aspect, as preserved in P.51263, Hajula, Lebanon. The suffixes 'r' and 'l' denote bones of the right and left side, explanation of other abbreviations p. 296.

Gaudryella in shape, but the sensory canal runs in a channel which is open ventrally, not in a closed tube, and there is no branch in the centre of the bone. The fourth and fifth infraorbitals (Io4, Io5, Figs. 19–21) together appear to be homologous with the fourth of *Gaudryella*. They extend back almost to the preopercular, but are less broad than the single bone in *Gaudryella*. In the fourth infraorbital, as in the third, the sensory canal ran in a channel which is open ventrally ; in the fifth the canal ran in a tube.

The dermosphenotic (Dsp, Figs. 15, 19) is elongate and triangular, containing a bone enclosed, triradiate sensory canal, as in *Gaudryella*, but the anterior limb of the bone is longer than in the latter, and the terminal branch of the infraorbital sensory canal within it expands as it passes forwards, and opens at the tip of the bone.

(iv) *Hyopalatine bones.* The hyomandibular (Hm, Figs. 19–21, 25 ; Fig. 22C) is broad and almost vertical. The head of the bone is single but constricted in the centre. As in *Gaudryella* the opercular process lies in the upper third of the bone, opposite the foramen for the hyomandibular trunk on the inner face of the bone. Antero-ventrally there is a deep notch separating an anterior membranous process from the ventral, endochondral part of the bone.

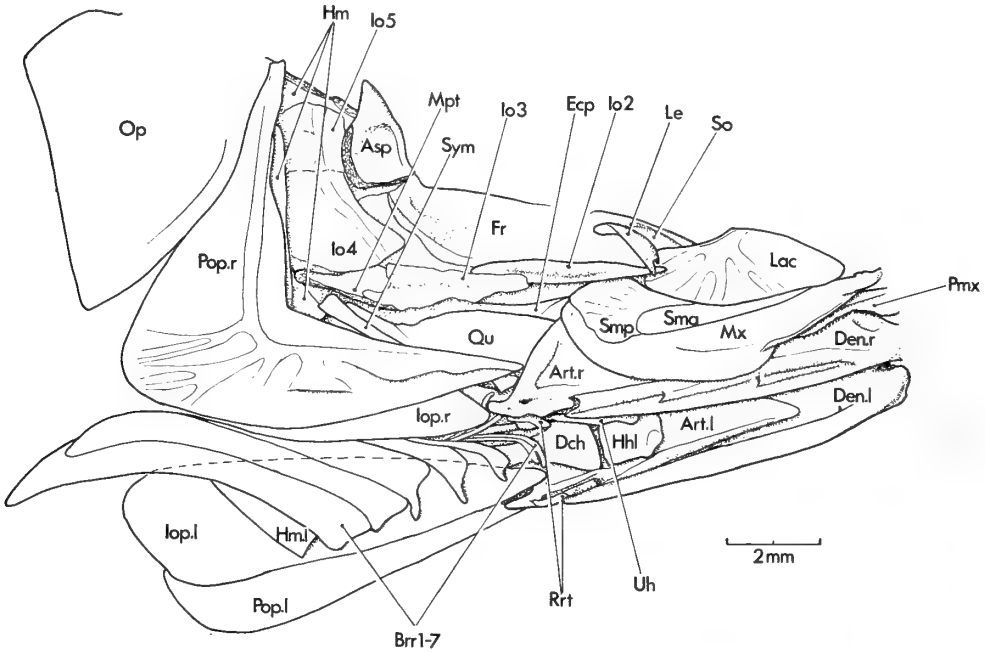

FIG. 21. *Humbertia operta* gen. & sp. nov. Skull crushed in ventro-lateral aspect, as preserved in AM 4590, Hajula, Lebanon. The left interopercular is drawn in transparency to show the heads of the branchiostegals. The suffixes ' r ' and ' l ' denote bones of the right and left side, explanation of other abbreviations p. 296.

The metapterygoid (Mpt, Figs. 19, 25) is larger than in *Gaudryella* and is visible in several specimens. In shape it resembles three-quarters of a circle, the upper posterior quadrant being missing. Ventrally it meets the quadrate, postero-dorsally it is overlapped by the hyomandibular, and dorsally it extends up over the medial surface of the endopterygoid, ending in a process which may have articulated with the basipterygoid process of the parasphenoid (see above).

As in *Gaudryella*, the symplectic (Sym, Figs. 20, 21, 25) is long and the quadrate (Qu, Figs. 19–21, 25) strongly inclined forwards, its condyle lying below the centre of

the orbit. The quadrate resembles that of *Gaudryella* but has a longer posterior process. The ectopterygoid (Ecp, Figs. 19–21) is slender, curved and toothless, as in *Gaudryella.* The endopterygoid is long and also toothless.

The palatine (Pal, Figs. 15, 22B) is straight and rather heavily ossified, as in *Gaudryella,* but differs from the latter in having a row of about ten small, recurved teeth. The head of the palatine has an antero-ventral knob (fvo) which articulates with the vomer, an elongate facet (fme), cartilage capped in life, above this which articulated with the ethmoid, and a smaller, lateral facet (fmx), also cartilage capped in life, which articulated with the palatine condyle on the maxilla.

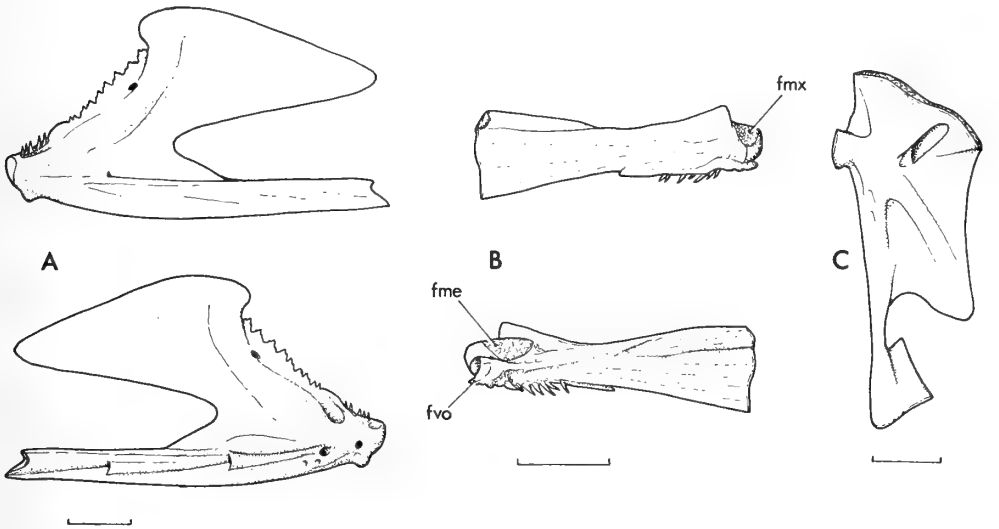

FIG. 22. *Humbertia operta* gen. & sp. nov. A, isolated right dentary, P.51267, in medial (above) and lateral view. B, isolated right palatine, P.51268, in lateral (above) and medial view. C, isolated left hyomandibular, P.51269, in medial view. All from Hajula, Lebanon. Scale 1 mm. *fme, fmx, fvo,* facets on palatine articulating with mesethmoid, maxilla and vomer.

(v) *Dermal upper jaw.* As in *Gaudryella,* the upper jaw contains the premaxilla, maxilla and two supramaxillae. The premaxilla (Pmx, Figs. 16, 19, 21 ; Fig. 23A,B) is equal in length to about 40% of the maxilla compared with about 25% in *Gaudryella:* both the proximal and distal extent of the premaxilla are greater than in *Gaudryella.* The oral border of the bone bears a single series of about twenty small, pointed teeth. Proximally the premaxilla bends medially and met its fellow in the mid-line, forming a blunt snout. This medial part of the premaxilla is toothless and forms a low, rounded ascending process (aspm), separated from the lateral part of the bone by a notch, which must have articulated with the mesethmoid or with a rostral cartilage. Lateral to the notch delimiting the ascending process there is an elongate knob on the inner face of the premaxilla, the articular process (arpm), which fitted in a depression just in front of and below the palatine condyle on the maxilla.

The maxilla (Mx, Figs. 15, 19–21 ; Fig. 23C) is similar in shape and size to that of *Gaudryella*. Proximally there is the usual cranial condyle (hmx) articulating with the mesethmoid, but the flange below the condyle, articulating with the vomer, is reduced in comparison with *Gaudryella*, and has a well marked facet laterally for the articular process of the premaxilla. The palatine condyle (pfmx) is similar to that of *Gaudryella*, but behind it the point of insertion of the palato-maxillary and posterior maxillo-mandibular ligaments is much less prominent than in *Gaudryella*. Above the posterior part of the premaxilla the ventral edge of the maxilla has a curious splint-like appearance, this ' splint ' extending a little way back as a lateral flange on the deep, posterior part of the maxilla (Figs. 19–21). Such a ' splint ' is not present in *Gaudryella*, or in any other teleost that I know : presumably it marks the insertion of a ligament or band of connective tissue. The oral border of the maxilla bears very small, clustered teeth which extend up the inner face of the bone a little, but are less numerous than in *Gaudryella*.

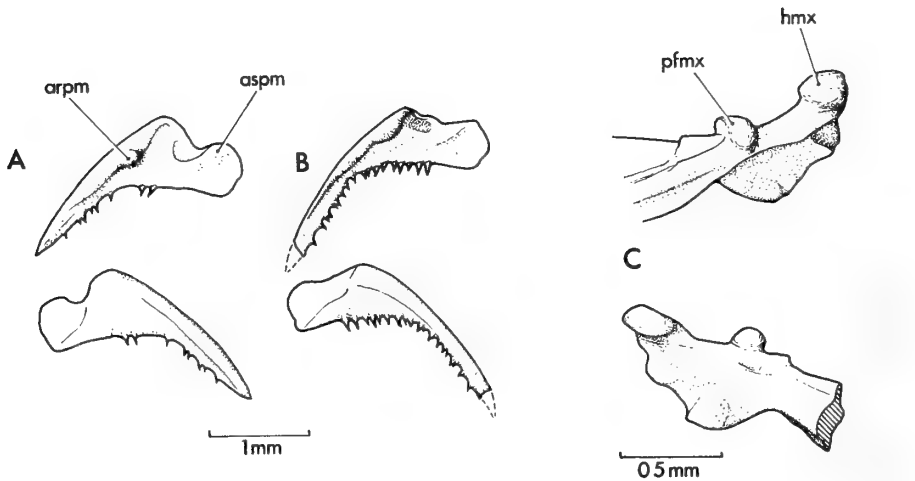

FIG. 23. *Humbertia operta* gen. & sp. nov. A,B, two isolated left premaxillae, P.51270–1, in internal (above) and external view. C, head of isolated right maxilla, P.51272, in external (above) and internal view. All from Hajula, Lebanon. Explanation of abbreviations p. 296.

The two supramaxillae (Sma, Smp, Figs. 20, 21) are essentially as in *Gaudryella*, except that the body of the posterior supramaxilla is shorter and deeper (cf. Figs. 5, 6, 9). As in *Gaudryella*, the supramaxillae were mobile, being displaced in fossils with the mouth open.

(vi) *Lower jaw*. The mandible is similar in shape to that of *Gaudryella*, with the same short, steeply ascending oral border, and long, high coronoid process. The dentary (Den, Figs. 19–21, 22A, 24, 25) differs from that of *Gaudryella* in having a shallower symphysis, without serrations, and a slightly less steeply ascending oral border which bears six to eight small, recurved teeth close to the symphysis followed

by a short, toothless diastema, and then by a single series of eight to ten blade-like teeth, increasing in size from front to rear, the larger teeth being serrated, with three to five minute cusps. These blade-like teeth are fused with the supporting bone and do not appear to be replaceable, but they have minute pulp cavities, consist of dentine and are true teeth, not serrations of the edge of the dentary. On the inner face of the dentary (Figs. 21, 22A) the pocket for the anterior end of Meckel's cartilage is extremely small, another striking difference from *Gaudryella*.

The angulo-articular (Art, Figs. 19–21, 25) and retroarticular (Rrt) appear to be indistinguishable from those of *Gaudryella*, and the course and distribution of pores and branches of the mandibular sensory canal in the angulo-articular and dentary are also as in *Gaudryella*. There is no sign of a sesamoid articular in the few specimens showing the medial face of the angulo-articular.

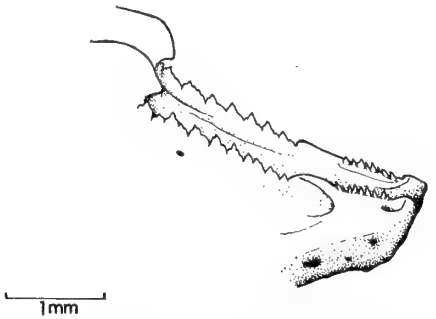

FIG. 24. *Humbertia operta* gen. & sp. nov. Anterior part of an isolated pair of dentaries, P.51273, in dorsal-lateral view to show the dentition. Hajula, Lebanon.

(vii) *Hyoid arch and branchiostegals.* The hyomandibular is described above, with the palate. The interhyal (Ih, Fig. 24) is short and waisted. The proximal and distal ceratohyals are similar to those of *Gaudryella* (Fig. 32), the proximal ossification (Pch, Figs. 20, 25) elongate and triangular, the distal (Dch, Figs. 20, 21, 25) deep and concave ventrally, both bones with a deep groove for the hyoidean artery on the outer face, the groove interrupted by an oval fenestra in the distal ossification. The main difference from *Gaudryella* is that the two ossifications, separated by cartilage in the latter, are sutured together by long, interdigitating spicules of bone on the inner surface (Fig. 20). The lower hypohyal (Hhl, Figs. 20, 21, 25) is large and square, the upper (Hhu, Fig. 25) small and containing a passage for the hyoidean artery. In front of the hypohyals one specimen shows a small endochondral ossification (Bh, Fig. 20), presumably a basihyal, but no other specimen shows a basihyal. There was no basihyal tooth plate. There is a long, slender urohyal (Uh, Figs. 20, 25) differing from that of *Gaudryella* in having shorter ventro-lateral laminae which are not concave anteriorly.

There are seven (normally) or eight branchiostegals (Figs. 20, 21, 32), the first two (or three where eight are present) slender and rod-like, the remainder curved and spathiform, their breadth increasing from front to rear, with ' clupeoid projections ' (McAllister 1968, fig. 1) at the bases of the last two. The last ray is extremely broad

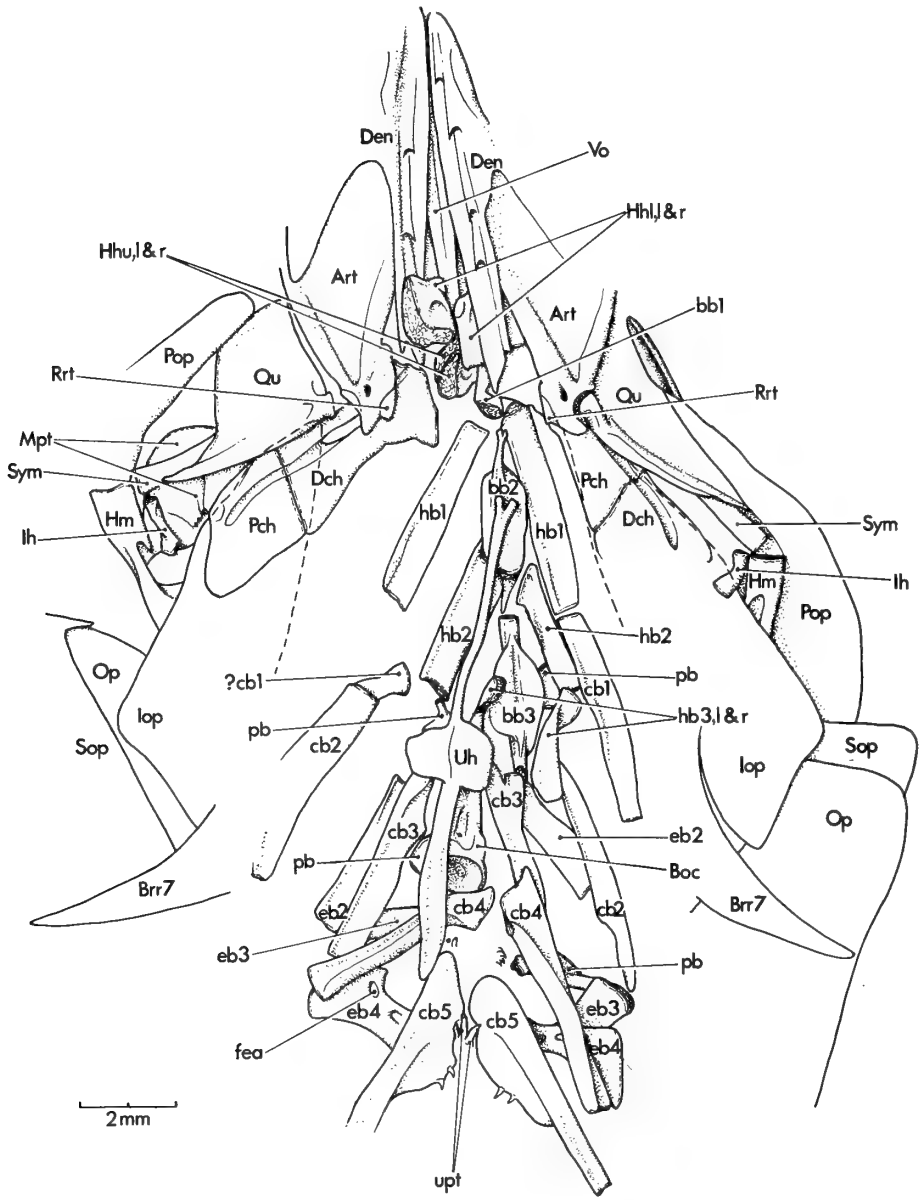

FIG. 25. *Humbertia operta* gen. & sp. nov. Dorso-ventrally crushed skull in ventral view showing the branchial skeleton. Simplified drawing of AM 4115, Hajula, Lebanon (cf. Pl. 5, fig. 1), branchiostegals omitted and anterior parts of left and right interoperculars drawn in transparency to show the ceratohyals. *bb* 1–3, basibranchials ; *cb* 1–5, ceratobranchials ; *eb* 2–4, epibranchials ; *fea*, efferent arterial foramen in fourth epibranchial ; *hb* 1–3, hypobranchials ; *pb*, pharyngobranchials ; *upt*, upper pharyngeal teeth ; explanation of other abbreviations p. 296.

and crescentic. The last two branchiostegals articulate with the outer face of the proximal ceratohyal, the next articulates on the suture between the proximal and distal ceratohyals, and the first four or five on the distal ceratohyal.

(viii) *Branchial arches.* One specimen, AM 4115 (Pl. 5, fig. 1 ; Fig. 25), shows much of the gill-arch skeleton in ventral view. Though the bones are badly crushed and displaced, it is possible to recognise most of the elements. There are three ossified basibranchials (bb 1–3), the first short and broad, the second and third long and slender but each bearing a broad dermal plate, apparently toothless, fused with the endochondral ossification. There are three pairs of hypobranchials (hb 1–3) the first and second long, the third shorter and twisted, with antero-ventral processes which probably formed a partial canal for the ventral aorta. The third hypobranchials, though shorter than the second, are longer than in most living teleosts, where they are usually small bones. The five ceratobranchials (cb 1–5) are long, as usual, and the fifth is fused with an oval tooth plate bearing rather large, conical teeth. The dorsal parts of the gill arches are mostly unrecognisable, but the deep, axe-head shaped fourth epibranchial (eb 4), apparently perforated by an efferent arterial foramen (fea), is conspicuous, and the second and third epibranchials (eb 2–3) can be tentatively identified. The upper pharyngeals bear large, conical teeth (upt), like the lower, but the details of their supporting bones cannot be seen, nor are the anterior pharyngobranchials (pb) certainly identifiable. The gill arches bear toothless, leaf-like gill-rakers, reaching about 1·5 mm. in length in a fish of 24 mm. head length, considerably smaller than in *Gaudryella*.

(ix) *Opercular bones.* The preopercular (Pop, Figs. 19–21, 25) is similar to that of *Gaudryella* in shape except that the vertical limb is proportionally longer. The vertical limb extends up to the pterotic and there was no suprapreopercular. As in *Gaudryella*, the preopercular sensory canal ran in a closed tube close to the anterior edge of the bone, but the branches at and below the angle are longer and more complex. There are three main branches of the canal at the angle, the uppermost short and bifurcated once, the next bifurcated twice and extending to the edge of the bone, the lowermost bifurcating three times and also extending to the edge of the bone (Fig. 20). Anterior to this there is one short, simple branch, and the anterior part of the canal ran in a groove which is open ventrally, as in *Gaudryella*.

The opercular (Op, Figs. 19–21, 25) and subopercular (Sop, Figs. 19, 20, 25) differ from those of *Gaudryella* chiefly in the much greater relative size of the subopercular: the suture between the opercular and subopercular lies at about 45° to the anterior edge of the opercular compared with about 65° in *Gaudryella*, and the area of the subopercular is about equal to that of the opercular. There is no ornament and no squamation on the operculum. The interopercular (Iop, Figs. 20, 21, 25) is very long, as in *Gaudryella*.

(x) *Vertebral column.* There are 36–39 vertebrae (normally 38) and a free second ural centrum (Fig. 33). Fourteen to seventeen vertebrae are caudal (normally 15), 22–24 abdominal (normally 23). The centra are perhaps more heavily ossified than in *Gaudryella*, with stronger ridges on the surface (cf. Figs. 13–14, 26–27), but are perforated by a notochordal canal. On the first 18–20 vertebrae the neural arches and parapophyses are autogenous (Fig. 18). All but the last two or three of these

autogenous neural arches are paired structures, the neural spines being paired also. As in *Gaudryella* there are about seven supraneurals above the anterior vertebrae. The epineurals are outgrowths of the neural arch on the first 12–15 vertebrae. On more posterior vertebrae the epineurals are free, their point of attachment rising on to the neural spine. The epineurals are rod-like, as in *Gaudryella*, but extend a little further back, usually to about the third caudal vertebra. As in *Gaudryella* there are no ribs on the first two vertebrae ; the ribs and parapophyses on the remaining abdominal vertebrae are similar to those of *Gaudryella* except that the parapophyses only increase in length on the last four vertebrae. There are rod-like epipleurals on the abdominal and first three or four caudal vertebrae. As in *Gaudryella*, the neural and haemal spines of pre-ural vertebrae 3–7 increase progressively in length and thickness, and the second pre-ural centrum has a low, broad neural spine. The caudal skeleton is described below, together with the caudal fin.

(xi) *Pectoral girdle and fin.* As in *Gaudryella*, the supratemporal (Stt, Figs. 15, 19) is a flimsy, scale-like bone, always more or less crushed into the post-temporal fossa. The bone is larger than that of *Gaudryella*, with its medial limb extending about halfway across the parietal. The sensory canal tube in the bone is triradiate, as usual, with a short antero-lateral limb, transmitting the temporal canal to the pterotic, and longer posterior and medial limbs. The medial branch of the canal, the supratemporal commissure, has two or three posteriorly directed branches, and leads into the transverse groove on the parietal.

The post-temporal (Ptt, Figs. 15, 19) resembles that of *Gaudryella* in shape, with the curved dorsal limb almost meeting its fellow above the supraoccipital, but the sensory canal gave off three to five dorsal branches in the bone, compared with two in *Gaudryella*. The supracleithrum (Scl, Fig. 19) is more slender than that of *Gaudryella* but otherwise similar, and the cleithrum (Cl, Fig. 19) shows nothing to distinguish it from that of *Gaudryella*. There are two postcleithra, the upper rectangular and plate-like, the lower rod-like with an expanded head, extending posteroventrally from the upper.

The endoskeletal pectoral girdle is partially visible in two specimens, but is poorly preserved and damaged in both. As in *Gaudryella* it consists of three ossifications, scapula, coracoid and mesocoracoid. The scapular foramen lies entirely within the scapula, and there is the usual large facet on the bone for the foremost fin-ray. The coracoid has a broad anterior process, and as far as it is visible seems to be like that of *Gaudryella*. The mesocoracoid is a narrow, arched strut on the inner face of the scapula and coracoid.

There are four proximal pectoral radials, similar in shape to those of *Gaudryella*. There is a series of distal pectoral radials, small nodular ossifications, apparently paired, lying between the bases of the fin-rays. There is a pair of distal radials between the hemitrichs of the first fin-ray, and at least three more pairs posteriorly.

The pectoral fin contains sixteen or seventeen rays, all segmented distally. The longest rays of the fin are equal in length to about seven vertebrae. As in *Gaudryella*, the upper hemitrich of the first ray is modified into a flat, scale-like structure, segmented distally. The base of this first upper hemitrich is also modified, being enlarged and perforated by a narrow canal.

(xii) *Pelvic girdle and fin.* The pelvic fins are inserted below the posterior part of the dorsal, at the level of the sixteenth or seventeenth vertebra. The pelvic girdle occupies a length of about four vertebrae, and appears to be identical with that of *Gaudryella*, except that the pelvic splint is separate, not fused with the girdle. There is no convincing evidence of ossified pelvic radials.

The pelvic fin contains a short, asymmetrical splint and twelve rays (four specimens and one fin of a fifth) or thirteen (one specimen and one fin of a second). All are segmented distally and the longest are equal in length to between five and six vertebrae, a little shorter than the pectoral rays.

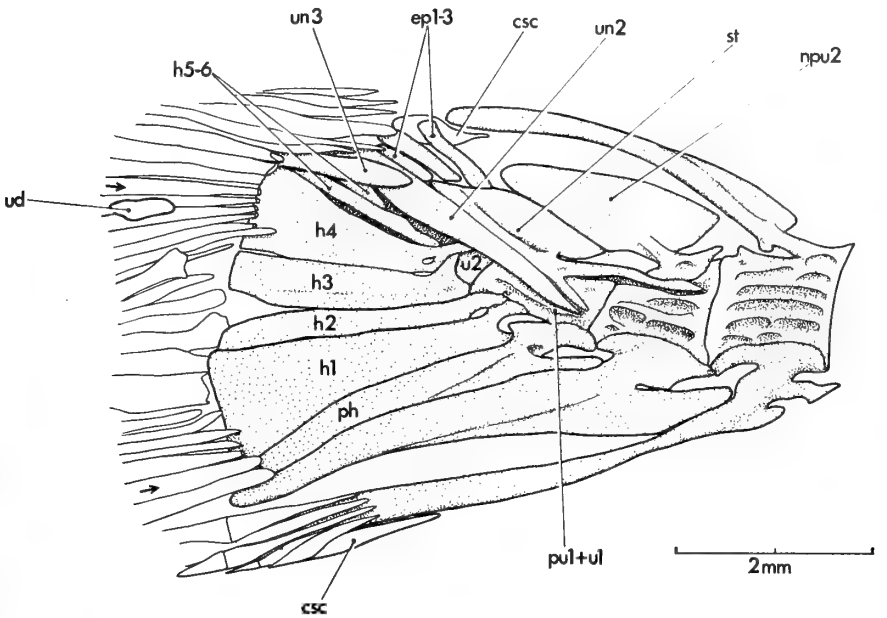

FIG. 26. *Humbertia operta* gen. & sp. nov. Caudal skeleton, slightly restored from P.48219 (holotype), Hakel, Lebanon. Arrows mark the outermost (unbranched) principal fin-rays, explanation of abbreviations p. 296.

(xiii) *Dorsal and anal fins.* The dorsal fin (Fig. 33) originates over the eleventh vertebra and occupies a length of about six vertebrae, lying just in front of the midpoint of the back. The fin contains fourteen rays supported by thirteen radials. The first two radials are crowded together and the first has a stout anterior process from its head. The shaft of the first radial ends above the ninth vertebra. Except for the first four, the radials have separate ossified middle segments. The first fin-ray is short and unsegmented, though paired. The remaining rays are all segmented distally, and all but the second and third are branched. The longest ray, the fourth, is equal in length to seven vertebrae, and about equal to the maximum depth of the trunk.

The anal fin (Fig. 33) is small and remote, as in *Gaudryella*, originating below the

ninth or tenth pre-ural vertebra and occupying a length of three vertebrae. The fin contains eight short, segmented rays supported by seven radials. The shaft of the first anal radial lies behind the haemal spine of the fourth caudal vertebra.

(xiv) *Caudal skeleton and fin.* The caudal skeleton (Figs. 26, 27) is less specialised than that of *Gaudryella*. The neural spines of PU3–5 are long and slightly expanded distally, and have laminar anterior expansions near their bases, growing larger from front to rear. These neural arches are not autogenous. The haemal spines of PU2–5 are similarly expanded distally, and there are anterior laminar expansions on those of PU2 and PU3. The haemal arches of PU2 and PU3 are always autogenous, that of PU4 is sometimes so. The foremost procurrent rays of the fin normally articulate with the neural spine of PU3 above and the haemal spine of PU3 or PU4 below, while the caudal scutes (csc, Fig. 27) extend forward to the neural spine of PU4 and the haemal spine of PU4 or PU5. PU2 has a low, leaf-like neural spine (npu2), as in *Gaudryella*, which is autogenous. The haemal spine of PU2 has a large anterior expansion and a smaller posterior one which fits closely against the anterior expansion of the parhypural, as in *Gaudryella*. The first pre-ural and ural centra are fused (pu1+u1), but in contrast to *Gaudryella* neither the parhypural, the lower hypurals nor the stegural is fused with this compound centrum. The parhypural (ph) has a hypurapophysis and an anterior expansion, paired at the base, articulating with the preceding haemal spine. The first hypural (h1) is very broad and articulates with the supporting centrum in the normal way. The slender second hypural (h2) is partially or completely fused with the first in about half the specimens, although in the remainder it is separate. This variation in the second hypural does not appear to be correlated with the size of the individual.

Articulating with the dorso-lateral surface of PU1 + U1 there is a large, autogenous stegural (st). The stegural consists of a shaft, forked proximally, and a dorso-medial expansion which extends forwards to fit against the neural spine of PU2, with a deep notch between it and the anterior part of the shaft of the bone. The upper fork of the stegural extends forwards across the dorso-lateral surface of PU2 and the short lower fork is applied to PU1 + U1, exactly as in *Elops* (Monod 1968, figs. 20–24) and *Nematonotus* (Patterson 1968b, fig. 25). The dorso-medial expansion of the stegural, representing the neural arches of PU1 and U1, seems to be very like that of *Gaudryella* (Fig. 13B), but it is not possible to tell whether the two stegurals are fused in the mid-line dorsally, as they are in *Gaudryella*. The second uroneural (un2) is similar to that of *Gaudryella* in length and position, but is broader. In contrast to *Gaudryella* there is a short third uroneural (un3) lying horizontally across the upper part of the second.

There is a small second ural centrum (u2), supporting four upper hypurals (h3–6). The third hypural is a little broader than the second, the fourth is almost as broad as the first, and the fifth and sixth are slender. As in *Gaudryella*, the head of the fifth hypural and the upper part of the head of the fourth extend forwards in slender points, dorso-lateral to the second ural centrum. There are three epurals (ep1–3), approximately equal in size.

The caudal fin is strongly forked and contains nineteen principal rays with seventeen branched. There are five to eight procurrent rays above and below, the first

two or three small, leaf-like and unsegmented. A rather large caudal scute (csc, Fig. 27) is present in front of both the upper and lower procurrent rays. As in *Gaudryella*, there is a single urodermal (ud) lying on the second ray below the uppermost principal ray.

(xv) *Squamation*. The scales are more clearly visible than those of *Gaudryella* and must have been thicker. As in *Gaudryella* they are acellular, large and cycloid, with continuous, well separated circuli. There appear to be eight scales in a transverse series on the trunk. There is a broad, continuous lateral line and as in *Gaudryella* the number of lateral line scales is approximately equal to the number of vertebrae. There are no scales on the cheek or operculum, and none on the bases of the fins.

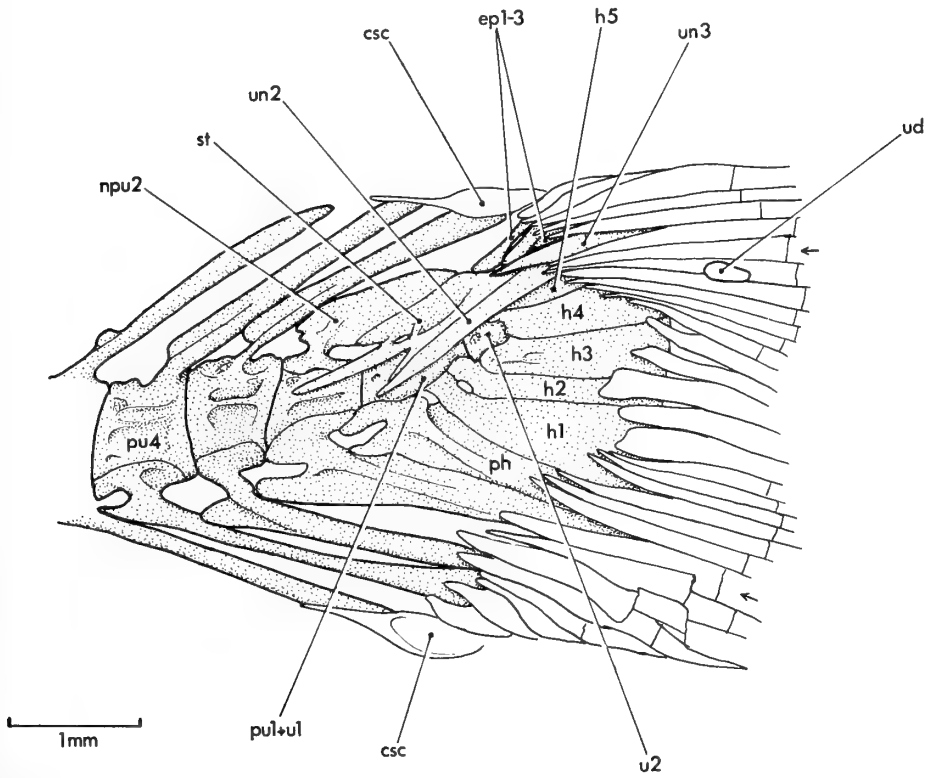

FIG. 27. *Humbertia operta* gen. & sp. nov. Caudal skeleton as preserved in AM 5564, Hajula, Lebanon. Arrows mark the outermost (unbranched) principal fin-rays, explanation of abbreviations p. 296.

(xvi) *Soft anatomy*. Muscle and retinal pigment are often preserved in the same manner as in *Gaudryella*, and fossilised gut contents (e.g. Pl. 4, fig. 2) show that the anus lay close in front of the anal fin. As in *Gaudryella* there is no evidence of an adipose fin. Chromatophores are sometimes preserved in specimens from Hajula as

pale spots under the scales : they indicate that the whole of the back was densely pigmented while the belly was light. The scales consist of acellular bone, but, as in *Gaudryella*, although most of the skeleton is also acellular, certain areas, mostly close to articular surfaces, contain many chondrocyte-like spaces. These areas include the head of the vomer, palatine and maxilla, the edge of the diastema on the dentary and the glenoid area of the endoskeletal pectoral girdle.

IV. DISCUSSION

(a) Similarities between *Gaudryella* and *Humbertia* and evidence of euteleostean relationships.

In addition to general similarities in size, body form, fin size and disposition, geological occurrence, etc., *Gaudryella gaudryi* and *Humbertia operta* share the following anatomical features :—

1. Supraoccipital small and parietals in contact medially
2. Post-temporal fossa roofed
3. Well developed bone-enclosed parietal and epiphyseal branches of supraorbital canal on frontal
4. Nasals slender and laterally placed
5. Large supraorbital and small, comma-shaped antorbital present
6. Trigemino-facialis chamber with three major external openings
7. Orbitosphenoid and basisphenoid well developed
8. Lachrymal large, second infraorbital slender, posterior infraorbitals extend to preopercular
9. Dermosphenotic large and triangular, the infraorbital sensory canal ending blindly anteriorly
10. Premaxilla small, maxilla with small, clustered teeth and bearing two mobile supramaxillae
11. Palatine without a maxillary process, with a ball and socket joint with the maxilla
12. Hyomandibular broad and vertical
13. Distal ceratohyal perforated by a fenestra
14. No scales on cheek or operculum
15. Anterior neural arches and parapophyses autogenous, anterior epineurals fused with neural arches
16. Seven or eight supraneurals above anterior vertebrae
17. Post-temporals almost in contact medially, attached to epiotics by ligaments
18. Mesocoracoid present, coracoid deep
19. Four proximal pectoral radials, several small distal radials
20. Pectoral fin low on flank, with about 16 rays, upper hemitrich of first ray laminar
21. Pelvics abdominal, with a splint and 12–13 rays
22. Anal fin small and remote
23. Scales large and cycloid, lateral line complete
24. Neural spine of second pre-ural centrum short and broad
25. Free second ural centrum present

26. First uroneural forked proximally
27. Caudal fin forked, with nineteen principal rays
28. Upper and lower caudal scutes and one urodermal present
29. Supratemporal a flimsy bone overlying post-temporal fossa, supratemporal commissure passes medially in a groove on the parietal
30. Vomer with a very long posterior process
31. Occipital condyle formed by basioccipital only
32. Intercalar small
33. Antorbital not penetrated or grooved by the infraorbital sensory canal
34. Symplectic and quadrate inclined forwards, mandibular articulation below centre of orbit.
35. Ectopterygoid and endopterygoid toothless
36. Dentary with a long, high coronoid process, with a deep pocket for the lip ligaments on its outer face
37. Urohyal very long and slender, with a broad, horizontal ventral flange
38. Toothless gill-rakers on gill arches
39. No ribs on first two vertebrae
40. Rod-like epipleurals on abdominal vertebrae
41. Two postcleithra, the upper scale-like, the lower rod-like
42. Anteriorly directed flanges on last two neural spines and last three haemal spines
43. First pre-ural and ural centra fused
44. Six hypurals, fifth and sixth with paired anterior processes alongside second ural centrum
45. First uroneural fused with neural arches of first ural and pre-ural centra to produce a stegural
46. Scales and most of skeleton acellular.

Of the characters in this list, numbers 1–28 are all probably primitive for teleosts (cf. leptolepids and pholidophorids, Rayner 1937 ; Nybelin 1962, 1966 ; Patterson 1967b, 1968a ; Wenz 1968 ; etc. : for the infraorbitals see Nelson 1969b ; for the maxillo-palatine joint see Schaeffer & Rosen 1961, Vrba 1968 ; for the ceratohyal see Rosen & Patterson 1969 : 408 ; for the second pre-ural neural spine see Patterson 1968b ; for the first uroneural Patterson 1968a). These primitive characters demonstrate that the two genera are teleosts of very primitive grade, but they are without much value in indicating relationships. Characters 29–46 are all probably advanced in some degree over the basic teleostean condition. The most significant of these advanced characters seem to be those of the caudal skeleton, numbers 42, 43 and 45. These three features, fusion of the first pre-ural and ural centra, the development of a stegural, and flanges on the last few neural and haemal spines (Gosline 1960 : 332) are each known to occur only in members of the Euteleostei (Greenwood *et al.* 1967). That this is the correct position of the two genera is also indicated by other advanced features such as the form of the supratemporal and supratemporal commissure (which passes through or over the supraoccipital in clupeomorphs, behind the parietal in elopiforms), the small intercalar (large and with an anterior strut across the subtemporal fossa in primitive osteoglossomorphs and elopomorphs), the absence of a

sensory canal in the antorbital (bone enclosed and with neuromasts in osteoglossomorphs and elopiforms : Nelson 1969b), the rod-like epipleurals (absent in osteoglossomorphs, usually forked in clupeomorphs), and the acellular bone of the skeleton (cellular in osteoglossomorphs, in elopiforms and eels amongst elopomorphs, and in almost all clupeomorphs : Kölliker 1859, Moss 1961).

Relationships with the euteleosteans are not opposed by any of the primitive characters common to *Gaudryella* and *Humbertia*, or by those known in only one of the two genera (such as the rudimentary basipterygoid process in *Humbertia* and the separate rostral of *Gaudryella*), for all are known to occur amongst generalised euteleosts in a mosaic distribution (a basipterygoid process is reported in the alepocephaloid *Searsia* by Gosline (1969 : 196) ; a perforate ceratohyal has not yet been recorded in primitive euteleosteans (see McAllister 1968) but is often present in *Coregonus* (Fig. 28)). Unfortunately, we do not know whether either fossil genus had an adipose fin, the chief distinguishing feature of generalised euteleosts.

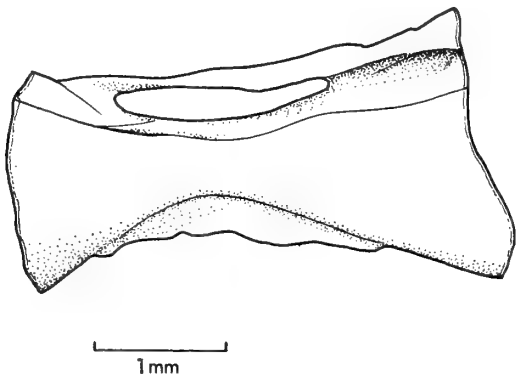

FIG. 28. *Coregonus lavaretus* L. Left distal ceratohyal of a 70 mm. individual in lateral view to show the fenestra. Recent, R. Gotha, Sweden, 1853.3.16.18.

(b) Differences between *Gaudryella* and *Humbertia* and relationships within the Euteleostei.

Amongst the Euteleostei, the area in which relatives of *Gaudryella* and *Humbertia* are to be found can be restricted to those groups in which the first ural and pre-ural centra are fused, i.e. the salmoniform suborders Argentinoidei, Galaxioidei, Osmeroidei and Stomiatoidei (the last two closely related according to Weitzman 1967b, but see Nelson 1970), the superorder Ostariophysi (including the gonorynchiforms, Rosen & Greenwood 1970), and the superorder Neoteleostei (ctenothrissiforms + myctophiforms + paracanthopterygians + acanthopterygians, Rosen & Patterson 1969 ; Nelson 1969a : 534).

The ostariophysans can be excluded from consideration for the following reasons :

1. There is no sign in *Gaudryella* and *Humbertia* of the anterior vertebral specialisations which characterise even the most primitive of these fishes (Rosen & Greenwood 1970 ; for the caudal skeleton see below, p. 276).

2. Ostariophysans are represented in the same beds as *Gaudryella* and *Humbertia*

by the gonorynchid *Charitosomus hakelensis*. This fish shows the typical jaws, pharyngeal teeth, caudal skeleton (Fig. 45), etc., of the gonorynchids, indicating that the gonorynchiforms (and therefore also the ostariophysans) were fully differentiated at that time.

3. The skeleton still consists of cellular bone in most members of both ostariophysan orders, and in the gonorynchiform *Chanos* (Kölliker 1959, Moss 1961 : *Charitosomus* appears to be acellular). *Gaudryella* and *Humbertia*, which are almost entirely acellular, are more advanced and can hardly be primitive members of this group.

The neoteleosts will also be left out of consideration, for reasons which are perhaps less convincing than those excluding the ostariophysans. In the same beds as *Gaudryella* and *Humbertia*, the neoteleosts are abundantly represented by myctophiforms (*Nematonotus* [Aulopidae], *Sardinioides* and *Cassandra* [? Neoscopelidae], *Acrognathus*), ctenothrissiforms (*Ctenothrissa*, *Pattersonichthys* [Goody 1969]) and acanthopterygians (*Hoplopteryx*, *Lissoberyx* [Trachichthyidae], *Stichocentus*, *Caproberyx* [Holocentridae], *Aipichthys*, *Pycnosteroides*). These fishes are easily recognisable, principally by the advanced position of the pelvics, the pectorals high on the flank, and the absence of a mesocoracoid. Lack of these specialisations in *Gaudryella* and *Humbertia* does not necessarily exclude these fishes from the Neoteleostei, but does mean that they could only be extremely primitive members of the group, especially in view of the structure of their jaws, palatine and ethmoid. In such a position it is improbable that the dentition would be as reduced as it is in *Gaudryella* and *Humbertia*, for primitive members of all major neotelostean lineages are notably well toothed on the jaws, palate, gill arches and gill-rakers, and also have a larger gape than *Gaudryella* and *Humbertia*. There are no advanced characters which definitely exclude *Gaudryella* or *Humbertia* from relationship with the neoteleosts, but they are certainly of more primitive grade than the latter. And whilst reduction of the gape and dentition in *Gaudryella* and *Humbertia* make such a relationship improbable, the absence in both of any of the advanced characters of the neoteleosts make further discussion of the possibility futile.

The remaining groups, the argentinoids, galaxioids, osmeroids and stomiatoids, are the only likely relatives of *Gaudryella* and *Humbertia*, and the two genera must be placed with them in the order Salmoniformes. None of these groups is reliably recorded in the Cretaceous. Osmeroids are first known in the Pleistocene, galaxioids in the Pliocene and argentinoids in the Oligocene. Various Cretaceous fishes have been placed in the Stomiatoidei, but these are critically discussed by Weitzman (1967b).

In considering these four salmoniform suborders, one is immediately struck by the many characters common to the two fossil genera and the argentinoids, especially *Argentina*. These include the body form, the size, composition and position of the fins (cf. illustrations in Cohen 1964), the large scales, reduced dentition, small jaws, short gape, long lower limb of the preopercular, long posterior process of the vomer, expanded posterior infraorbitals, structure of the skull roof, with the parietals in contact, the post-temporal fossa roofed and similar frontals (cf. Figs. 3A, 29A ; and illustrations in Chapman 1942a, b, 1943, 1948), and the vertebrae, where the epineurals

are fused with the autogenous neural arches anteriorly, the parapophyses are autogenous, and epipleurals are present (at least in *Argentina*). However, in argentinoids there are marginal vomerine teeth (central and longitudinal in *Gaudryella*, absent in *Humbertia*), the basihyal (Nelson 1970) is long and primitively toothed (short in *Gaudryella*, toothless in *Humbertia*), the premaxilla and maxilla are toothless, and there are no supramaxillae. Also, in *Argentina*, one of the most primitive genera, the skeleton is cellular (Kölliker 1959 ; personal observations), and even in *Bathylagus*, which is advanced in having the parietals separate, no mesocoracoid, no swim-

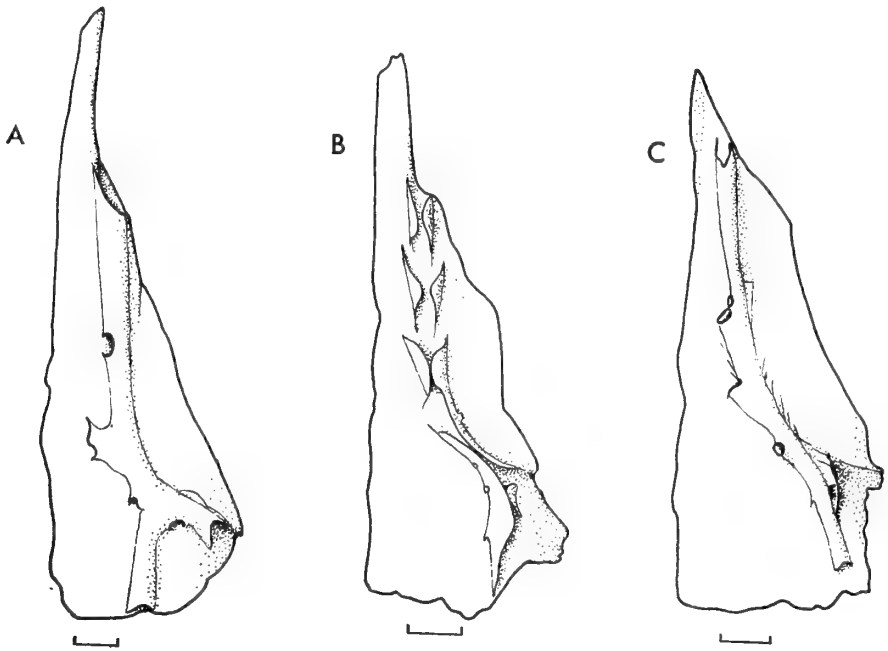

FIG. 29. Right frontals in dorsal view of A, *Argentina sialis* Gilbert, Recent, N.E. Pacific, 1967.3.5.2, 72 mm. ; B, *Hypomesus olidus* (Pallas), Recent, Tartar Strait, 1925.8.6.9, 93 mm. ; C, *Coregonus lavaretus* L., same specimen as Fig. 28. Scale 1 mm.

bladder, etc., the skeleton is still cellular (personal observation). This suggests that all argentinoids retain cellular bone and are therefore more primitive than the almost acellular *Gaudryella* and *Humbertia*.

The osmeroids and stomiatoids are acellular, like *Gaudryella* and *Humbertia*, but are primitively well toothed forms, with endopterygoid, basihyal and basibranchial teeth. In this they are more primitive than *Gaudryella* and *Humbertia*, while they are more advanced in having slender posterior infraorbitals, the neural arches and parapophyses fused with the centra (except in *Plecoglossus*, Weitzman 1967b : 531), no orbitosphenoid, etc.

The galaxioids have recently been revised by McDowall (1969) and shown to comprise two groups, one containing the galaxiids and aplochitonids, the other the

TABLE 3

Differences between *Gaudryella gaudryi* and *Humbertia operta*

Character	*Gaudryella gaudryi*	*Humbertia operta*
1. Maximum standard length	90 mm	115 mm
2. Parietals	Almost square, groove for supratemporal commissure short and shallow	Shorter and broader, groove for supratemporal commissure longer and deeper
3. Nasals	Short, trough-like	Long, tubular
4. Ethmoid	Rostral and mesethmoid separate, triradiate anteriorly, rostral overlying frontals posteriorly	Rostral and mesethmoid fused, disc-like anteriorly, underlying frontals posteriorly
5. Vomer	Narrow, with a median row of teeth	Broader, toothless
6. Parasphenoid	Notched by efferent pseudobranchial artery, without basipterygoid process	Pierced by efferent pseudobranchial artery, with rudimentary basiptergoid process
7. Posterior infraorbitals	One large bone	Two bones
8. Head of hyomandibular	Double	Single
9. Metapterygoid	Reduced	Normal
10. Palatine	Toothless	Toothed
11. Premaxilla	25% length of maxilla, toothless, without distinguishable ascending and articular processes	40% length of maxilla, toothed, with rudimentary ascending and articular processes
12. Symphyseal end of dentary	Serrated	Smooth
13. Oral margin of dentary	With a few small teeth near symphysis	Small teeth near symphysis, larger, blade-like teeth behind
14. Inner face of dentary	With large pocket for tip of angulo-articular	With minute pocket for Meckel's cartilage
15. Distal and proximal ceratohyals	Separated by cartilage	Sutured together on medial surface
16. Basihyal	Unossified, covered by toothplate	Small ossification, no toothplate
17. Branchiostegals	11, last two spathiform	7–8, last five spathiform, crescentic posteriorly
18. Branches of preopercular sensory canal	Short	Long, dichotomising
19. Subopercular	Upper edge at 25°, smaller than opercular	Upper edge at 45°, about as large as opercular
20. Vertebrae	mean 43, 28 + 15	mean 38, 23 + 15
21. Autogenous neural arches	12–15	18–20
22. Epineurals fused with neural arches	8–10	12–15
23. Branches of sensory canal in supra- and post-temporal	2 ; none	3–5 ; 2–3
24. Origin of pelvic fin	below vertebra 21	below vertebra 16
25. Pelvic splint	fused with girdle	autogenous
26. Origin of dorsal fin	over vertebra 15–16	over vertebra 11
27. Dorsal fin	12 rays, 12 radials, last radial with no fin-ray	14 rays, 13 radials

Table 3—*continued*

Character	*Gaudryella gaudryi*	*Humbertia operta*
28. Anal fin	9 rays, 8 radials	8 rays, 7 radials
29. Lamellar expansions on last few neural and haemal spines	on NPU2–3, HPU2	on NPU2–5, HPU2–3
30. Parhypural and lower hypurals	fused with centrum and each other	autogenous
31. Hypurals three and four	partially fused	separate
32. Stegural	fused with centrum	autogenous
33. Third uroneural	absent	present
34. Epurals	2	3
35. Caudal scutes	small	large
36. Scales	very thin	thicker

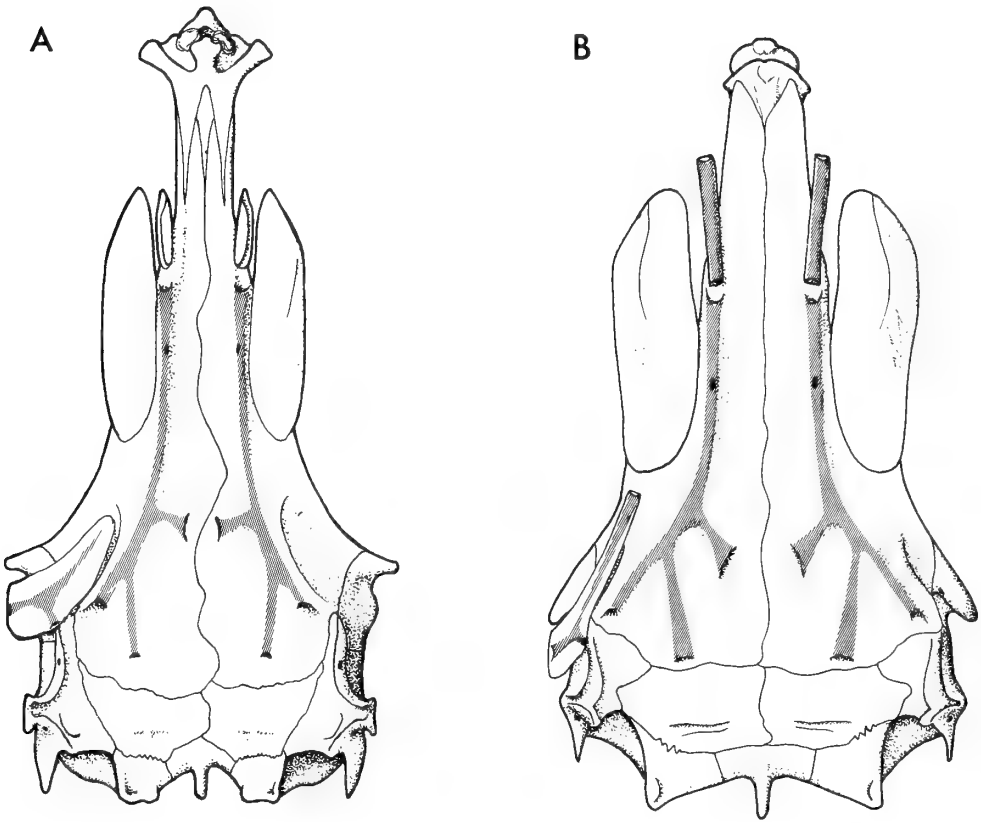

FIG. 30. Restorations of skull roof in dorsal view, A, *Gaudryella gaudryi* (Pictet & Humbert), B, *Humbertia operta* gen. & sp. nov. Both × 6 approx. Bone-enclosed sensory canals cross-hatched. Both Middle Cenomanian, Hakel and Hajula, Lebanon.

retropinnids and prototroctids. Galaxioids are acellular, but have a low, well toothed mandible and endopterygoid teeth. They are advanced over *Gaudryella* and *Humbertia* in many ways, notably in having the ectopterygoid reduced or absent, a

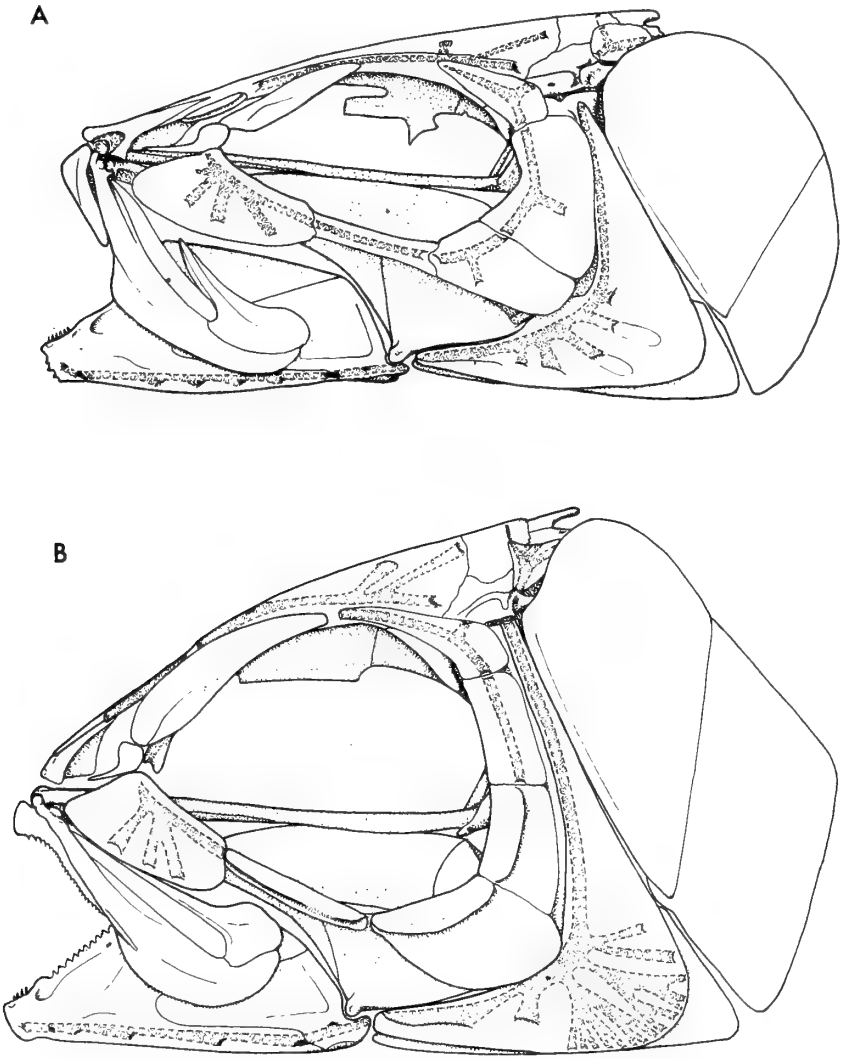

FIG. 31. Restorations of skull in lateral view, A, *Gaudryella gaudryi* (Pictet & Humbert), B, *Humbertia operta* gen. & sp. nov. Both × 5 approx., Middle Cenomanian, Hakel and Hajula, Lebanon.

narrow or incomplete infraorbital series, no supramaxillae, orbitosphenoid or mesocoracoid, the neural arches and parapophyses fused with the centra, and less than nineteen principal caudal rays.

Before discussing these and other resemblances, it is necessary to consider the differences between *Gaudryella* and *Humbertia*, which are listed in Table 3 and summarised in Figs. 30–33.

Many of these differences appear relatively trivial, such as are commonly found within a genus or family. Others are surely of greater significance, such as the structure of the ethmoid region (4), parasphenoid (6), infraorbitals (7), jaws and dentition (5, 10, 11, 12, 13, 16), hyoid and branchiostegals (15, 16, 17), operculum (19) and caudal skeleton (30–34). In the parasphenoid, infraorbitals, toothed palatine and premaxilla, large subopercular, several features of the caudal skeleton, and in various minor features such as those of the vertebrae and the more numerous, bone-enclosed branches of the sensory canals, *Humbertia* is the more primitive of the two

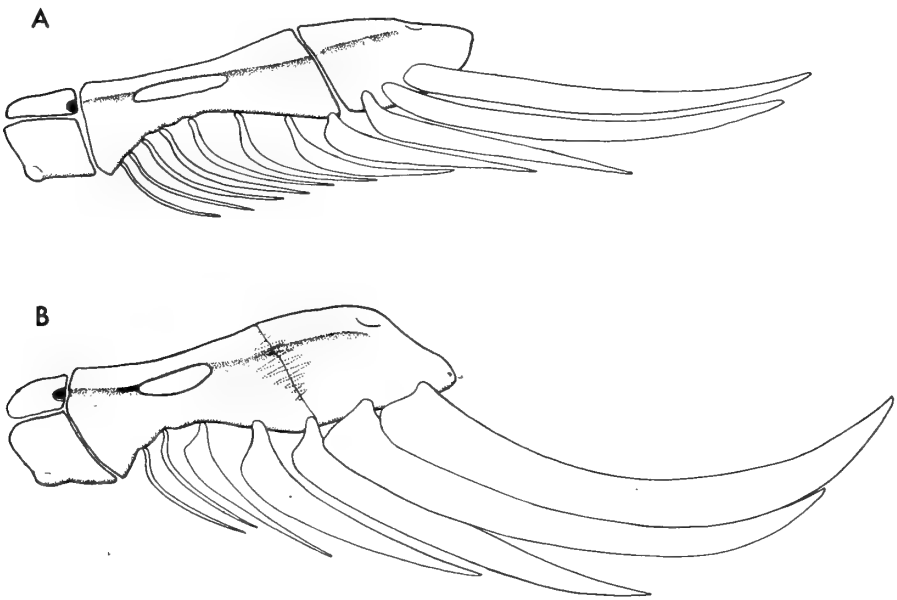

FIG. 32. Restorations of left hyoid bar and branchiostegals in lateral view, A, *Gaudryella gaudryi* (Pictet & Humbert), B, *Humbertia operta* gen. & sp. nov. Both × 8 approx., Middle Cenomanian, Hakel and Hajula, Lebanon. The dotted line across the ceratohyal in B indicates the splints of bone suturing the distal and proximal ceratohyals on the medial surface.

(for the subopercular cf. leptolepids and pholidophorids, Nybelin 1962, 1966), but in the ethmoid (see below), toothed vomer and basihyal, and in the hyoid and branchiostegals, *Gaudryella* is more primitive, showing that there can be no close relationship of ancestor-descendant type between the two. There is little that can be said about some of these differences, such as those concerning the specialisations of the posterior infraorbitals and pelvic spint in *Gaudryella*, since in both these features it is unique, so far as I know (for the infraorbitals, cf. Nelson 1969b). Other

major differences will be discussed in relation to the conditions in argentinoids, galaxioids, osmeroids and stomiatoids.

(i) *Ethmoid region*

Weitzman (1967b) has recently discussed the ethmoid ossifications of salmoniform fishes but in view of his conclusions further consideration of these bones is necessary, although the evidence on which my own opinions are mainly based, the structure of the ethmoid region in Jurassic pholidophorids and leptolepids, will be presented fully elsewhere. Weitzman concluded (pp. 524, 527) that the pattern of ethmoid bones found in the osmerid *Spirinchus* is primitive for salmoniforms. In *Spirinchus* there are seven laminar ethmoid bones : paired proethmoids and capsular ethmoids, and median supraethmoid, ventral ethmoid and anterior myodome bones. The proethmoids are superficial and presumably dermal, the remainder are perichondral ossifications of the ethmoid cartilage. There is no endochondral ossification. Weitzman finds this pattern to be primitive because it is complete in what he believes is the most primitive osmerid and is little modified in primitive stomiatoids, more so in advanced ones. Weitzman does not discuss the alternative view, that these numerous ethmoid bones are the result of fragmentation, writing only that such a hypothesis 'seems untenable' : I would maintain it, however. The opposing hypotheses of fusion and fragmentation in various parts of the fish skeleton have been widely discussed, with regard to the dermal bones (e.g., Devillers & Corsin 1968, Ørvig 1968) and the endoskeleton (e.g., Jarvik 1954, 1965, Nelson 1969a). In the snout of actinopterygians it is now well established that the overall trend throughout the evolution of the group has been towards fragmentation, not fusion, in both the dermal bones (Gardiner 1963) and the endoskeleton (Nielsen 1942, 1949). In discussing the details of the ethmoid ossifications in teleosts and their forerunners it is necessary first to distinguish between dermal bones and the endoskeleton, although this is often very difficult, even when careful embryological work has been done (e.g. in *Salmo*, see Pehrson 1944 : 146 ; de Beer 1937 : 126).

The *dermal skeleton* of the ethmoid region is primitively formed in teleosts by only one dorsal bone, the rostral, primitively separate from the underlying endoskeleton and enclosing the ethmoid commissure, which may be subsequently reduced to a pit-line. Whether the rostral of the teleost lineage was originally paired or unpaired is not yet known (see Griffith & Patterson 1963 : 34), and perhaps such a question has little meaning since in *Lepisosteus* (Hammarberg 1937 : 287) and *Amia* (Pehrson 1940 : 9) the rostral develops from paired rudiments which soon fuse to produce the median rostral characteristic of the adult fish. The paired origin of the rostral in ontogeny is due to the influence of the invaginated neuromasts of the ethmoid commissure, which are paired. Pehrson's study of the embryology of *Esox* (1944) shows that the paired proethmoids of this fish are undoubtedly homologous with the median, canal-bearing rostral of holosteans and primitive teleosts, since the proethmoids originate in relation to the organs of the ethmoid commissure, here reduced to a pit-line. Presumably, only when the influence of the sense organs declines further can the rostral originate as a median bone, as it does in *Salmo* (Pehrson 1944 : 145 ; Devillers 1948 : 39) and many higher teleosts. Further evidence of the homology of

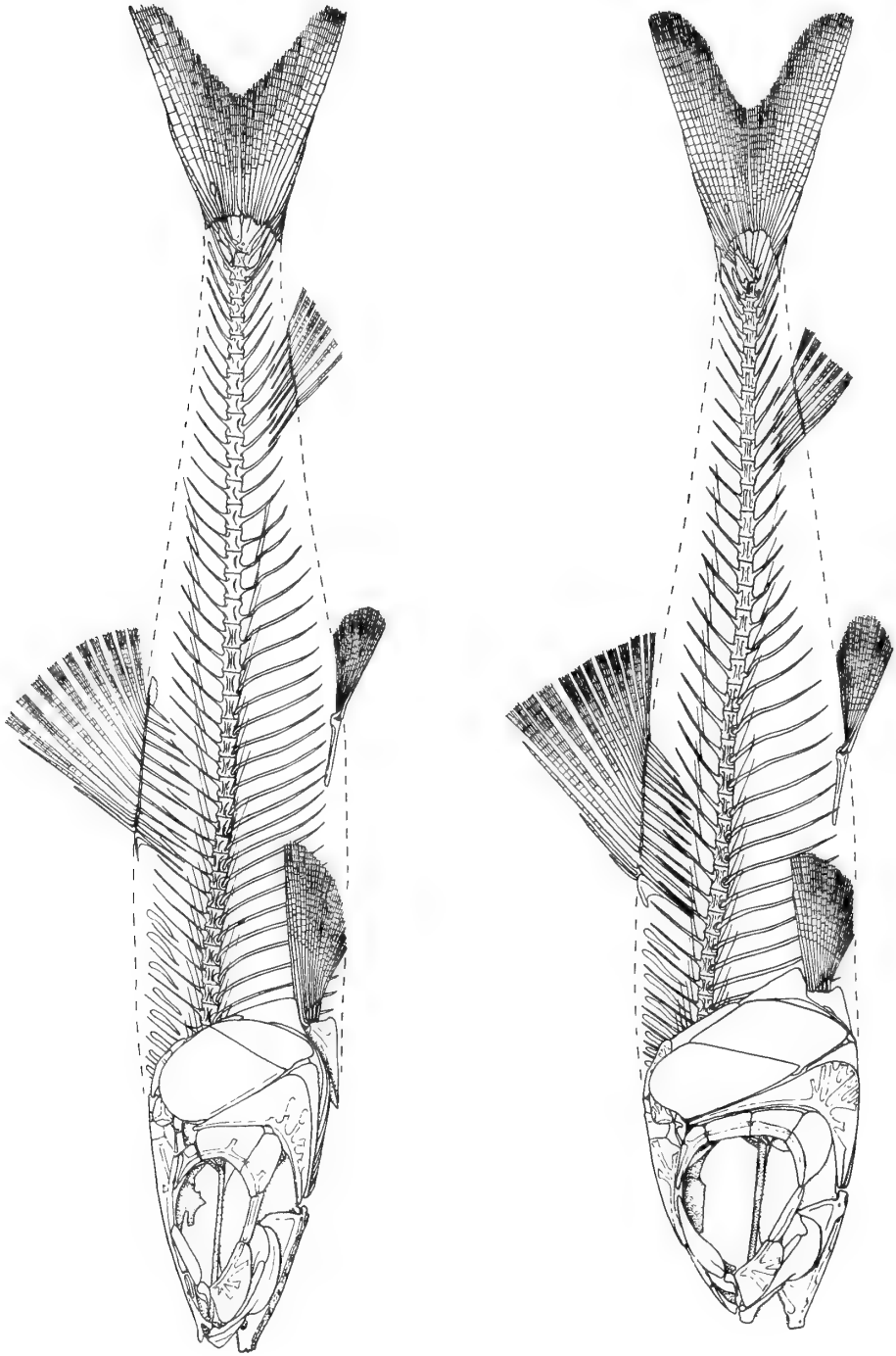

FIG. 33. Restorations of the skeleton, scales omitted, of *Gaudryella gaudryi* (Pictet & Humbert) (above) and *Humbertia operta* gen. & sp. nov. (below). Both × 2½ approx., Middle Cenomanian, Hakel and Hajula, Lebanon.

paired proethmoids and a median rostral is furnished by the identical morphological relationships of the proethmoids in osmerids such as *Spirinchus* and *Thaleichthys* compared with the median rostral of the osmerid *Hypomesus*.

In all the pholidophorids that I have examined the rostral is a broad, shield-like, unpaired bone, carrying a bone-enclosed ethmoid commissure whose width is about equal to the distance between the left and right posterior nostrils (see also Nybelin 1966 ; 1967a, fig. 1 A–C). In the Lower Jurassic *Leptolepis coryphaenoides* the rostral is already fused with the underlying endoskeletal ossifications (Rayner 1937 ; Wenz 1968 : 202 ; personal observations) and the ethmoid commissure is very short (Fig. 34). Wenz, with abundant material of *L. coryphaenoides*, finds that the ethmoid commissure may be bone-enclosed or a pit-line, and more significantly that the rostral, usually unpaired, is frequently divided by a median suture (1968, fig. 89). I have not observed this condition with certainty in *L. coryphaenoides* (ten ethmoids available), nor in the Upper Jurassic *L. sprattiformis*, where Wenz (1968 : 204) finds a paired

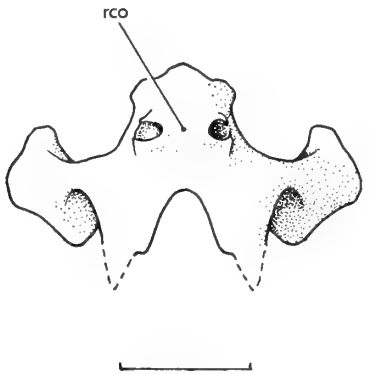

FIG. 34. *Leptolepis* sp. Isolated rostral in dorsal view, restoration based on P.51288, from stomach contents of a *Pholidophorus*, Oxfordian (Upper Jurassic), Dives, Normandy, France. Scale 1 mm. *rco*, rostral commissure.

rostral to be a constant feature, and indeed it is difficult to see how paired rostrals could exist when the rostral is already fused with the endoskeleton. But if Wenz is correct in these observations, *L. coryphaenoides* provides the earliest evidence of the existence of proethmoids, and that proethmoids and a median rostral should exist in the same species is further indication that there is no essential difference between the two conditions. Amongst living teleosts, all those with a bone-enclosed ethmoid commissure have a median rostral. Only in forms where the commissure has been reduced to a pit-line (or lost) do paired proethmoids appear (esocoids, some osmerids and stomiatoids).

In search of homologues of the proethmoids amongst other primitive teleosts, Weitzman (1967b: 526) refers to the ventro-lateral processes of the rostral in *Megalops* (Fig. 35A), which cap the cartilagenous anterior walls of the nasal capsules, and in large individuals meet an anterior process of the lateral ethmoid below the nasal capsule.

Weitzman suggests that fusion between these processes and the body of the rostral is incomplete in small specimens (36–75 mm.) and considers it possible that they are independent ossifications. Although these processes are absent in *Elops*, they are present in the Upper Jurassic *Anaethalion* (Nybelin 1967b, pl. 7, pl. 8, figs. 1, 2), which appears to be a close relative of the elopoids. Exactly similar ventro-lateral processes are also present in the Jurassic leptolepids (Wenz 1968, figs. 84, 89 ; Fig. 34). In *L. coryphaenoides* (Upper Lias) they are continuous with the rostral and partially fused with the underlying peri- and endochondral bone. But in a primitive, undescribed leptolepid from the Lower Lias this process is apparently separate from the rostral, extending towards the mid-line below it. The process is underlain by a distinct layer of perichondral bone and is therefore presumably dermal in origin. After removal of the rostral in this primitive leptolepid these processes are strikingly similar to the 'proethmoids ' of the stomiatoid *Polymetme* (Weitzman 1967b, fig. 12). These lateral processes therefore appear to be distinct from the rostral in *Megalops* and in early leptolepids. They can hardly be considered part of the rostral since in *Megalops* they are overlain by a separate, canal-bearing lateral rostral (Nybelin 1967a, fig. 2B, C). Berg (1955, figs. 190, 191) found a pair of small, presumably dermal bones (' parethmoid ') lying lateral to the rostral in *Coregonus lavaretus*. I have not found these bones myself, nor were they present in any of the eight North American species of *Coregonus* investigated by Norden (1961), but they might be relevant to the lateral processes of the rostral. The problem of the origin of this apparently dermal lateral process is analogous to the question of the existence of a dermal ' prefrontal ', which some investigators have found as a separate element in embryos of *Amia* and various teleosts, later fusing with the perichondral lateral ethmoid. As in the case of the lateral process of the rostral, there is no dermal bone in more primitive actinopterygians with which a prefrontal can be satisfactorily homologised.

While it is obvious that there are many unsolved problems in the dermal bones of the ethmoid region of teleosts, some conclusions can be listed by way of summary :

1. The unpaired, canal-bearing rostral of pholidophoroids, leptolepids and elopoids is homologous with the unpaired dermal bone below the ethmoid pit-line in salmonids, some osmerids, etc. ; with the superficial part of the compound mesethmoid of many higher teleosts ; and with the paired proethmoids of esocoids, some osmerids and stomiatoids.

2. The rostral is primitively separate from the underlying peri- and endochondral ossifications, and fusion between the two is an advanced feature.

3. No decision is possible on whether the rostral is primitively paired (proethmoids) or median (rostral), but in those teleosts where proethmoids are present (esocoids, osmerids, stomiatoids) they appear to be a neotenous character associated with the persistent influence of the sense organs of the ethmoid commissure.

4. The lateral processes of the rostral in *Megalops* and leptolepids may primitively have been independent ossifications whose origin is unknown.

The *endoskeleton* of the ethmoid region in palaeoniscoids and various ' subholosteans ' is part of a single, massive ossification, extending back to the occipital fissure (Nielsen 1942, 1949 ; Rayner 1948, 1951 ; Lehman 1952). In the Lower Triassic parasemionotids, sutures appear separating a preorbital ossification from

an orbito-temporal (Lehman 1952, fig. 105), and a similar single preorbital ossification is found in the Jurassic ' holosteans ' *Caturus*, *Aspidorhynchus* (Rayner 1948) and *Heterolepidotus* (personal observation). In the Upper Jurassic pholidophoroid *Ichthyokentema* the preorbital region is also occupied by a single large ossification (Griffith & Patterson 1963), but in pholidophorids there are usually three ossifications, paired lateral ethmoids and a mesethmoid, as in leptolepids and most living teleosts.

In many primitive living teleosts the endoskeleton of the ethmoid region is very poorly ossified (elopiforms, salmonines, *Chanos*, osmerids, etc.) ; a heavily ossified ethmoid is more common in higher groups such as the ostariophysans, myctophiforms and acanthopterygians. This has led Starks (1926), Weitzman (1967b) and others to the conclusion that a lightly or superficially ossified ethmoid is the primitive condition in teleosts, a reversal of the trend exemplified by the fossil evidence summarised above. Weitzman surmises that endochondral bone was re-introduced and that separate perichondral bones fused in several groups as adaptations to increased mobility or power of the jaws. But on this hypothesis one would predict that such fishes as the leptolepids, small, primitive and almost edentulous teleosts which were certainly microphagous, should have a very lightly ossified ethmoid region. In fact this is not so : in the more primitive leptolepids the mesethmoid is a solid mass of endochondral bone. A heavily ossified mesethmoid is also the rule in Cretaceous teleosts, irrespective of the form of the jaws (Patterson 1964, Goody 1969). In the endoskeleton of the gill arches, Nelson (1969a : 521) concludes that ' there is no known example of simple fusion between separate bones or ossification centres ', and one might expect the same to be true of the neurocranium.

The alternative hypothesis, advocated here, is that a heavily ossified mesethmoid is primitive for teleosts, in agreement with the general trend in actinopterygians (and other fishes) and with the evidence of fossil teleosts. One would then assume that in certain groups such as osmerids and stomiatoids the reduction in ossification of the ethmoid has proceeded further in the more primitive members, perhaps because they have more lightly toothed or less mobile jaws. The several ethmoid ossifications of primitive osmerids and stomiatoids would thus be an advanced feature providing evidence that the two groups are related, which they would not do if Weitzman's assumptions were correct.

Weitzman predicted (1967b : 527) that the five perichondral ethmoid bones of some osmerids and stomiatoids (supraethmoid, ventral ethmoid, anterior myodome bones and capsular ethmoids) will be found in some pholidophoroid. This is so, but they are not separate ossifications. The endochondral bone of the mesethmoid in leptolepids and pholidophorids is surrounded by continuous perichondral bone, whose upper, lower and lateral surfaces are respectively homologues of the supraethmoid, ventral ethmoid and capsular ethmoids. I have not yet seen an anterior myodome bone in any leptolepid, but one is present as a hollow cone of perichondral bone on the posterior surface of the mesethmoid in *Pholidophorus germanicus* (Lower Jurassic) and *P. macrocephalus* (Upper Jurassic).

In summary, the evidence is that the primitive condition of the ethmoid endoskeleton in teleosts is to have a median mesethmoid and paired lateral ethmoids, each well ossified in endochondral and perichondral bone. Reduction of endochondral bone

followed by reduction of perichondral bone has occurred in many lineages, in some groups resulting in several separate perichondral ossifications.

This rather lengthy preamble is necessary before the structure of the ethmoid region in *Gaudryella* and *Humbertia* can be discussed. Of the two, *Gaudryella* is the more primitive in having the dermal skeleton (rostral) and endoskeleton (mesethmoid) still separate. The rostral of *Gaudryella* (Fig. 2) is strikingly like those of *Leptolepis* (Fig. 34) and *Megalops* (Fig. 35A), and I have little doubt that the lateral processes of the rostral in the three, though slightly different in form, are homologous.

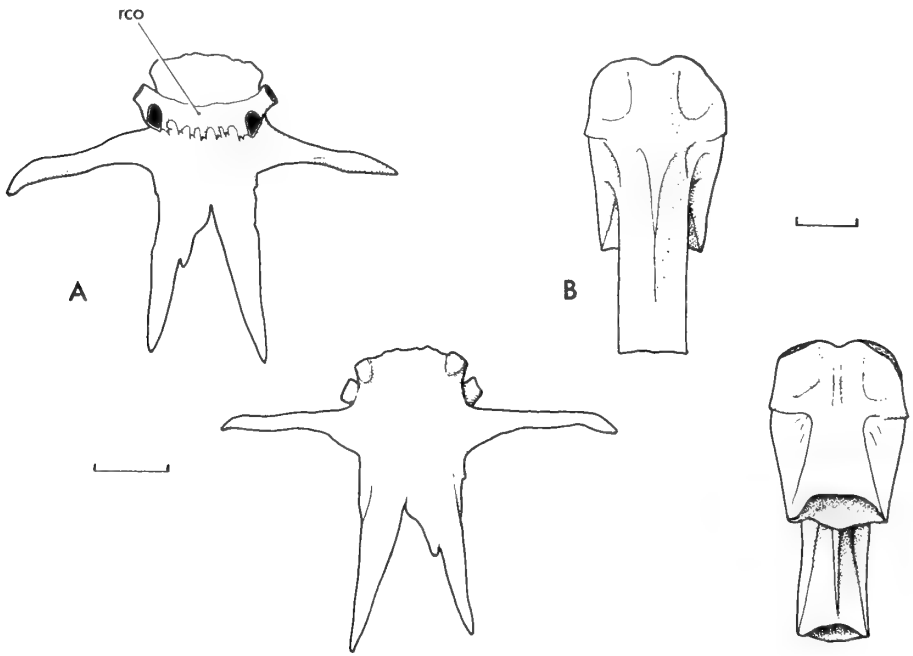

FIG. 35. A, *Megalops cyprinoides* (Broussonet), rostral of a 90 mm. individual in dorsal (above) and ventral view, 1855.9.19.832. B, *Argentina sialis* Gilbert, mesethmoid of a 72 mm. individual in dorsal (above) and ventral view, same specimen as Fig. 29A. Scale 1 mm.

Gaudryella is more advanced than *Leptolepis* and *Megalops* in having no impression on the bone of the ethmoid commissure or pit-line, but is more primitive than *Megalops* in having a well ossified mesethmoid below the rostral, and more primitive than most leptolepids in having the rostral and mesethmoid unfused. Apart from the loss or reduction of the ethmoid commissure, therefore, the ethmoid region of *Gaudryella* is one of the most primitive known amongst teleosts. All euteleosteans are more advanced in this region, and even those which still retain separate rostral and mesethmoid ossifications (coregonines, esocoids, osmerids, some stomiatoids) have the mesethmoid poorly ossified and the rostral (or proethmoids) usually short and plate-like. The proethmoids of the stomiatoid *Polymetme* (Weitzman 1967b,

fig. 12) are reminiscent of the anterior part of the rostral of *Gaudryella*, and the proethmoids of some esocoids extend back over the frontals like the rostral of *Gaudryella*, but there seem to be no other similarities worth comment. Although the ethmoid ossifications of *Gaudryella* are too primitive to be readily compared with those of any euteleostean, this does not mean that the fish may not be related to some living group in which these ossifications are more advanced.

In *Humbertia* the body of the mesethmoid (Fig. 16) is rather similar to the endoskeletal mesethmoid of *Gaudryella* but less heavily ossified, while the long, membranous posterior processes are presumably the homologues of the posterior processes of the rostral in *Gaudryella*, although in *Humbertia* they lie below, not above the frontals. In having the dermal and endoskeletal components of the ethmoid ossification fused, *Humbertia* is more advanced than the coregonines, esocoids, osmerids and primitive stomiatoids, in which the two remain separate, while in the rather flimsy, lightly ossified mesethmoid *Humbertia* is more advanced than generalised ostariophysans and neoteleosts. Among primitive euteleosteans, the closest approach to the mesethmoid of *Humbertia* seems to be in *Argentina* (Fig. 35B), where the degree of ossification and the shape are very similar, except that the long posterior processes are lacking.

(ii) *Jaws and dentition*

In *Gaudryella* the vomer is toothed, the palatine and premaxilla are toothless, the premaxilla is short and has no distinguishable articular and ascending processes, the dentary is toothed only near the symphysis, and the basihyal is toothed. In *Humbertia* the vomer and basihyal are toothless, the palatine and premaxilla are toothed, the premaxilla is rather long and has rudimentary articular and ascending processes, and the dentary has blade-like teeth along most of its oral border. Also, *Humbertia* has rather large pharyngeal teeth but pharyngeal teeth have never been seen in *Gaudryella*. These rather profound differences, like those in the ethmoid region, are surely correlated with different feeding methods, although it is not possible to speculate on the different habits involved. But the differences in the dentition suggest that *Gaudryella*, with its few teeth placed on or near the mid-line, has the primary bite between the toothed vomer and tongue, as in argentinoids and coregonines, while *Humbertia* has a primary grasping or holding bite between the toothed dermal upper and lower jaws, and a secondary gulping bite between the pharyngeals, as in myctophiforms and higher teleosts.

The simple, toothless premaxilla of *Gaudryella* (Fig. 7A) resembles those of the argentinoids, but is even simpler than these (Fig. 36A), which have at least a distinct articular process (arpm). The premaxilla of *Humbertia* (Fig. 23) is very like those of osmerids, especially *Hypomesus* (Fig. 36B). The maxillae and supramaxillae of *Gaudryella* and *Humbertia* are very similar, and are so primitive (cf. elopoids, clupeoids) that little can be said of them. The only other euteleosteans with two supramaxillae are the alepocephaloids, some stomiatoids, and primitive neoteleosts.

The lower jaw is similar in shape in *Gaudryella* (Fig. 8) and *Humbertia* (Fig. 22A), with a long, steeply ascending coronoid process, concave anteriorly. A coronoid process of this type has been used by palaeontologists as a character of various taxa and as evidence of various supposed phyletic lines. Dr. P. H. Greenwood has sug-

gested to me that a lower jaw of this type may be merely a ' grade ' character, presumably adaptive, in primitive teleosts. This interpretation is certainly supported by the distribution of this type of mandible, which is found in *Ichthyokentema*, *Leptolepis*, *Allothrissops*, *Pachythrissops*, *Clupavus*, *Ctenothrissa*, some clupeoids, *Coregonus*, *Hypomesus*, *Chanos*, some cyprinoids, etc., the dentition ranging from bands of small teeth along the whole oral border (*Pachythrissops*) to nothing (*Chanos*, *Clupavus*, cyprinoids). It is clear from this list that the shape of the lower jaw can hardly be used as evidence of relationship. In *Gaudryella* the mandibular dentition is much reduced, as in some *Leptolepis*, *Coregonus* and *Hypomesus* (Fig. 37B). The mandibular dentition of *Humbertia* (Fig. 24), with small anterior teeth and a short diastema followed by a series of blade-like, serrated teeth, is very unusual. The closest approach to it seems to be among the argentinoids, where the mandibular teeth are blade-like, in a single row, and apparently fused to the bone in microstomatines, and in *Bathylagus* (Fig. 37A) are similar but show a progressive increase in size from front to rear, with traces of serration on the larger posterior teeth.

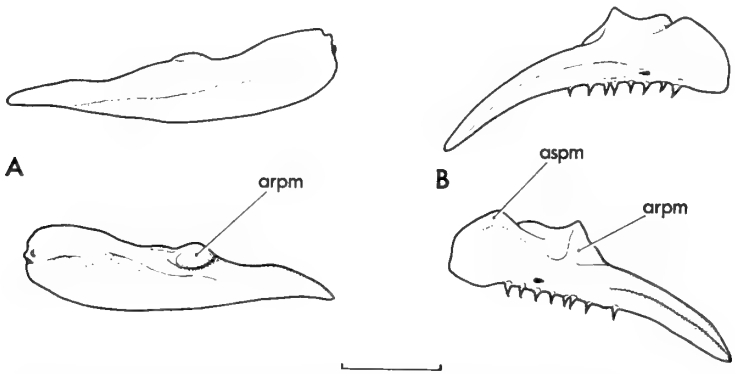

FIG. 36. Right premaxillae in external (above) and internal view of A, *Argentina sialis* Gilbert, Recent, N.E. Pacific, 1967.3.5.2, 87 mm. ; B, *Hypomesus olidus* (Pallas), Recent, same specimen as Fig. 29B. Scale 1 mm. Explanation of abbreviations p. 296.

Weitzman (1967b : 529) has drawn attention to the recess on the inner face of the dentary which houses the anterior end of Meckel's cartilage and the angulo-articular, and the insertion of the adductor mandibulae muscle. He concludes that a large recess, opening far back, as in some osmeroids and stomiatoids, is primitive for teleosts. Weitzman notes that the recess is small or absent in galaxioids, salmonids and esocoids, but large and posterior in some alepocephaloids, myctophoids, and in *Elops* and *Megalops*. Among early fossil teleosts, the pholidophorids, which have a somewhat *Amia*-like mandible, have no such recess in the dentary. *Leptolepis coryphaenoides* and other early leptolepids have a very minute recess, about as in *Humbertia* (Fig. 22A), while the Upper Jurassic *L. dubius* has a slightly larger recess. The Upper Jurassic *Anaethalion*, which is very similar to *Elops* (Nybelin 1967b), has a much smaller recess than *Elops* : in the best preserved *Anaethalion* specimen available to me the recess opens at a point distant from the symphysis by 28% of the total

length of the mandible, while in *Elops* it opens almost exactly midway along the mandible. This evidence indicates that the recess on the inner face of the dentary is a structure which has appeared within the teleosts, and that a small, anteriorly placed recess is therefore primitive. The large, posteriorly placed recess of osmeroids and stomiatoids would then be another advanced character indicating that the two groups are related. *Hypomesus* (Fig. 37B), however, is an osmerid with a small, anteriorly placed recess. The recess is extremely small in *Humbertia*, resembling that of early leptolepids, and is probably primitive. *Gaudryella* has a fairly large recess, about as in *Argentina* among argentinoids, *Mallotus* among osmerids.

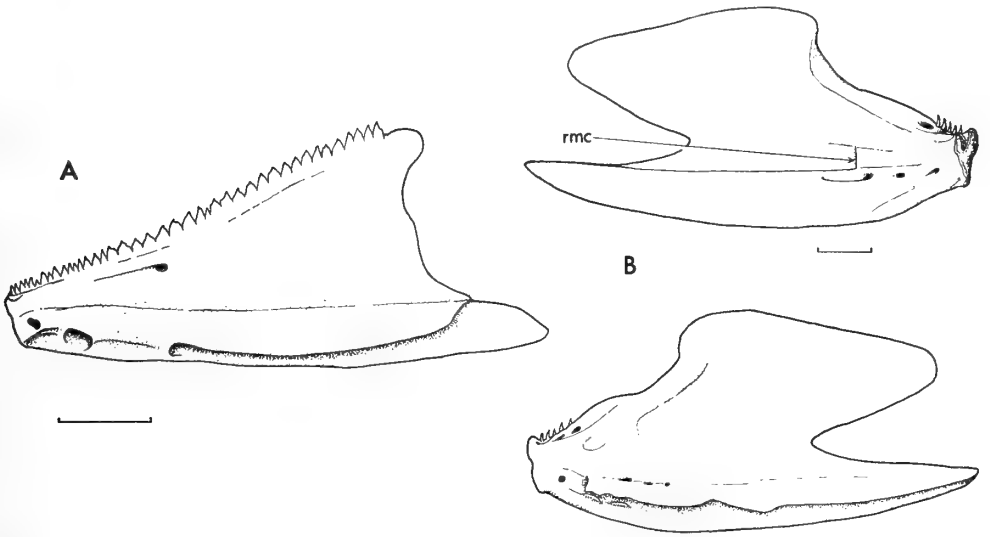

FIG. 37. Left dentaries of A, *Bathylagus antarcticus* Günther in lateral view, Recent, ' Discovery ' station 298, 85 mm. ; B, *Hypomesus olidus* (Pallas) in medial (above) and lateral view, same specimen as Fig. 29B. Scale 1 mm. *rmc*, recess housing Meckel's cartilage.

In the palate, *Gaudryella* and *Humbertia* differ from osmeroids, stomiatoids and galaxioids in the complete absence of endopterygoid teeth. The lack of ectopterygoid teeth in *Gaudryella* and *Humbertia* is typical of salmoniforms : amongst euteleosteans, ectopterygoid teeth occur only in neotelosts and in a few characoids (Weitzman 1967b : 529). The metapterygoid of *Humbertia* is normal and unremarkable, but the reduced metapterygoid of *Gaudryella* resembles that bone in argentinoids (Chapman 1948).

The shaft of the vomer is probably primitively moderately long, as it is in *Pholidophorus germanicus*, *Leptolepis* (Patterson 1967b, fig. 5 ; and observations on other species), *Elops*, *Alepocephalus*, etc. The very long shaft seen in argentinoids, *Gaudryella* and *Humbertia* and the complete absence of a shaft in osmerids, *Retropinna*, *Prototroctes*, etc., are probably divergent specialisations which tend to align *Gaudryella* and *Humbertia* with the argentinoids.

Restriction of teeth to the margin of the basihyal tooth plate in *Gaudryella* is a feature typical of salmonoid, argentinoid, osmeroid and galaxioid salmoniforms, but not of stomiatoids or esocoids (Nelson 1970). In lacking a dermal basihyal plate, *Humbertia* differs from primitive members of all these groups.

In summary, the jaws and palate of *Gaudryella* and *Humbertia* are closest to those of argentinoids, especially in the long vomer and toothless endopterygoid of both genera, the premaxilla and reduced metapterygoid of *Gaudryella*, and the mandibular dentition of *Humbertia*. But neither genus shows the marginal vomerine teeth and elongate basihyal tooth plate which are so characteristic of argentinoids. Apart from the features mentioned here, the jaws and palate of *Gaudryella* and *Humbertia* are too generalised to be much help in deciding on relationships. Although there are marked differences between the two genera in the jaws and palate, I cannot find that these show one genus to be closer to any group than is the other.

(iii) *Hyoid and branchiostegals*

In the perforate ceratohyal, *Gaudryella* and *Humbertia* are more primitive than any known euteleosteans except *Coregonus* (Fig. 28) and some neoteleost groups (ctenothrissiforms, primitive paracanthopterygians and acanthopterygians). But the fenestra in the ceratohyal has been lost independently in many groups and no particular significance can be attached to it.

The two ossifications of the ceratohyal are separated by cartilage in *Gaudryella*, as they are in all primitive teleosts according to McAllister (1968, table 1). In *Humbertia* the two ossifications are sutured together by splints on their inner faces. McAllister finds this to be an advanced character, independently acquired in siluroid ostariophysans and in neoteleosts, where it first occurs in *Ctenothrissa*, is absent in beryciforms and commonly occurs in both acanthopterygians and paracanthopterygians. I cannot see that the suture in *Humbertia* is anything but a further example of independent acquisition of the feature.

Gaudryella has eleven branchiostegals, all slender and almost straight (acinaciform) except for the last two, which are spathiform and curved distally (Fig. 32A). *Humbertia* has seven or eight branchiostegals of which the last five are broad and spathiform, the last two being especially broad and strongly curved, with ' clupeoid projections ' at their bases (Fig. 32B). The distribution of spathiform branchiostegals (McAllister 1968, table 1) shows that this is undoubtedly the primitive condition in actinopterygians, while ' clupeoid projections ', which occur in clupeoids, bathylaconids (Alepocephaloidei), osmerids, chanoids, characoids and cyprinoids, seem to be a character of primitive teleostean groups in which the branchiostegal number is low. The pattern of the branchiostegals in *Gaudryella* and *Humbertia* is similar to those of argentinoids, osmeroids, stomiatoids and galaxioids. *Gaudryella* has more numerous branchiostegals than argentinoids (2–7), osmeroids (4–10) and galaxioids (3–9), but fewer than many stomiatoids (5–24). The branchiostegals of stomiatoids are shorter than those of *Gaudryella*, those of galaxioids are straighter. In general, the branchiostegals of *Gaudryella* seem closest to those of osmerids. *Humbertia* has fewer branchiostegals than some osmeroids, stomiatoids and galaxioids. In number and shape of the branchiostegals *Humbertia* is close to *Argentina* (7 rays), but the last rays

of this genus are neither so broad nor so strongly curved as in *Humbertia*. The osmeroid *Plecoglossus* (6 rays) has very broad, crescentic posterior branchiostegals, as in *Humbertia*.

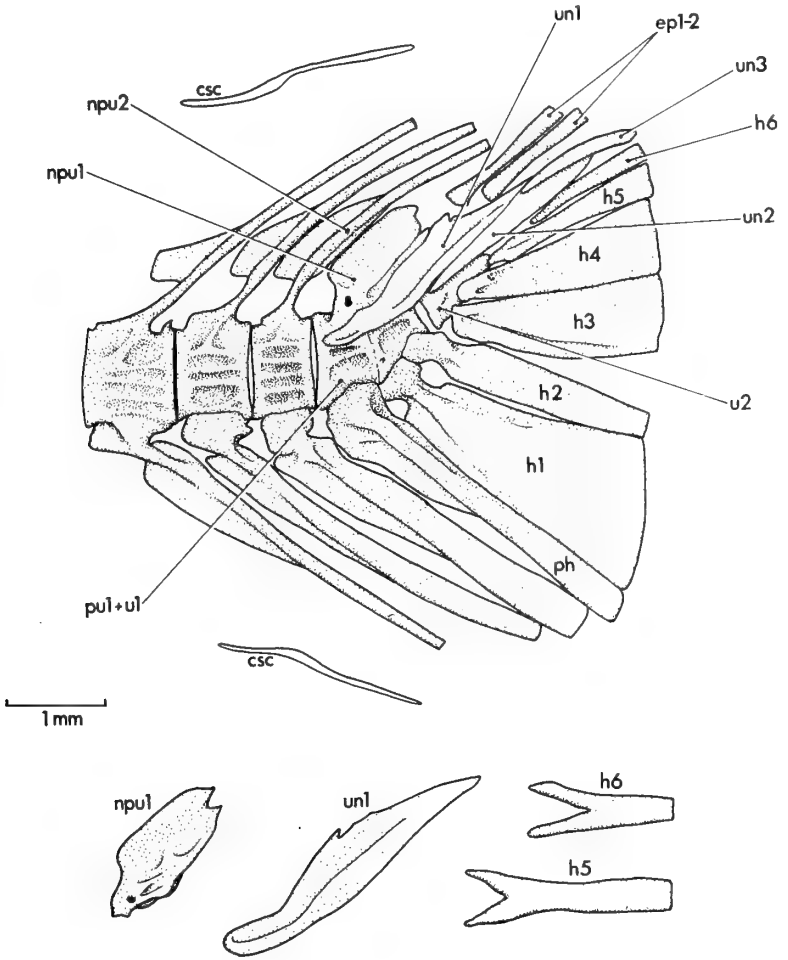

FIG. 38. *Argentina sialis* Gilbert, Recent. Above, caudal skeleton of a stained and cleared specimen (same specimen as Fig. 36A) ; below, detached bones of a macerated specimen from the same lot (same specimen as Fig. 29A), the first pre-ural neural spine and first uroneural in lateral view (the neural spine broken from the centrum), the fifth and sixth hypurals in dorsal view. Explanation of abbreviations p. 296.

(iv) *Caudal skeleton*

As noted above, fusion of the first pre-ural and ural centra is known only in the argentinoids, galaxioids, osmeroids, stomiatoids, ostariophysans and neoteleosts. Caudal structures in these groups will be discussed in relation to the conditions in *Gaudryella* and *Humbertia*.

Amongst argentinoids, caudal skeletons have been illustrated in *Opisthoproctus* (Trewavas 1933, pl. 2 ; Parr 1937, fig. 13), *Bathylagus* (Beebe 1933, fig. 41), *Macropinna* (Chapman 1942a, fig. 6), *Nansenia* (Chapman 1948, fig. 12) and *Argentina* (Gosline 1960, fig. 10 ; Rosen & Patterson 1969, fig. 71). *Microstoma*, *Bathylagus* and *Argentina* are illustrated here (Figs. 38–41). In *Opisthoproctus* and *Macropinna* the illustrations by Trewavas, Chapman and Parr all seem to show separate centra supporting the parhypural and the lower hypurals, and alizarin preparations of two specimens of *Opisthoproctus* in the American Museum of Natural History show that PU1 and U1 are separate. In other argentinoids the compound centrum (PU1 + U1) is very long, as in *Humbertia* (Figs. 26, 27), and in *Argentina* there are often surface markings (Rosen & Patterson 1969, fig. 71 ; Fig. 38) suggesting that two centra have fused during ontogeny, though they are not separable, even under heavy maceration. There are six hypurals in argentinoids, as in *Gaudryella* and *Humbertia*, and there is a free second ural centrum in *Argentina* (Fig. 38), *Microstoma* (Fig. 39), *Macropinna* and

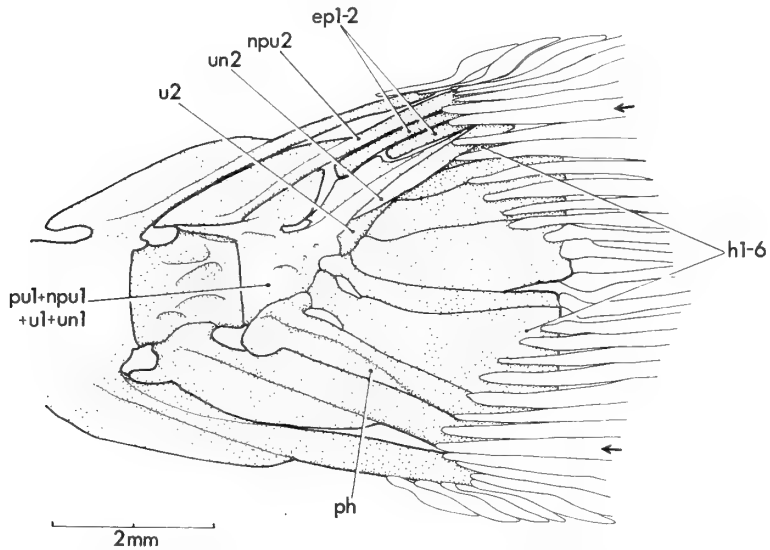

FIG. 39. *Microstoma microstoma* (Risso), Recent. Caudal skeleton of a dried skeleton, 1888.11.29.67, 150 mm., Mediterranean. Arrows mark the outermost (unbranched) principal fin-rays, explanation of abbreviations p. 296.

Bathylagus (Fig. 41), where it is much reduced and not visible externally. In *Nansenia* Chapman's figure shows no U2, but dissected specimens have a small one, much as in *Bathylagus*. *Argentina*, *Bathylagus*, *Microstoma* and *Opisthoproctus* have a full neural spine on PU2, but in *Macropinna* and *Nansenia* Chapman's illustrations show a low, broad neural spine, as in *Gaudryella* and *Humbertia*. However, in two dissected specimens of *Nansenia groenlandica* there is a full neural spine on PU2, and since other features lead one to mistrust Chapman's drawings of caudal skeletons it appears that a full neural spine on PU2 is characteristic of argentinoids. All argentinoids have two or fewer epurals. In *Argentina* there are three uroneurals, large

caudal scutes, and a urodermal (Rosen & Patterson 1969, fig. 71). *Opisthoproctus* also has a urodermal (D. E. Rosen, pers. commn.). *Bathylagus* (Fig. 40) also has three uroneurals, but no caudal scutes or urodermal, and the first uroneural is fused with the supporting compound centrum. In *Microstoma* (Fig. 39) there are only two uroneurals, the first fused with the compound centrum. The illustrated specimen of *Microstoma* is of interest in having the first uroneural produced forwards across PU2, as it is in *Gaudryella* and *Humbertia*, but this projection

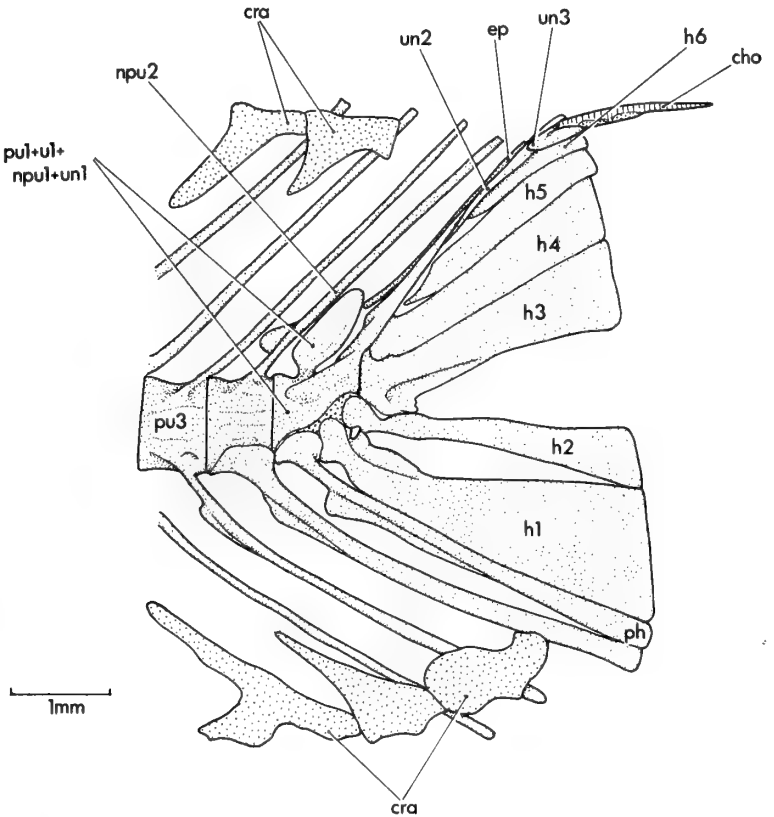

FIG. 40. *Bathylagus antarcticus* Günther, Recent. Caudal skeleton of a dissected specimen, 100 mm., same lot as Fig. 37A. *cho*, notochord ; *cra*, cartilages supporting the procurrent caudal rays (the last upper cartilage removed) ; explanation of other abbreviations p. 296.

is missing on the right side of the specimen. In *Bathylagus* and especially in *Microstoma* fusion of the first uroneural with the compound centrum produces a caudal skeleton resembling that of *Gaudryella* (Figs. 13, 14), but the caudal skeleton of *Argentina* disposes of this apparent similarity. Gosline's figure (1960, fig. 10) of a large dried skeleton of *Argentina silus* (standard length c. 33 cm.) shows a suture

between the first uroneural (UN1) and the neural arch of the compound centrum (NA). Maceration of a 75 mm. specimen of *A. sialis* (Fig. 38) shows that this is correct : the first uroneural (un1) is quite separate from the neural arch (npu1), which is fused with the compound centrum. In *Bathylagus*, although the lower part of the first uroneural is fused with the compound centrum, the neural arch of that centrum (which may be double, Fig. 41) is quite distinct from the uroneural. This shows that in argentinoids the neural arch of the compound centrum, NPU1 (or NPU1 and NU1 where the arch is double) fused first with the centrum, not with the first uroneural. Argentinoids therefore never had a true stegural, taking the stegural to be the first uroneural fused with the neural arches of PU1 and U1 (Patterson 1968a : 229 ; 1968b : 50). The implications of this are discussed further below, but it immediately excludes the argentinoids from relationship with *Gaudryella* and *Humbertia*, in which a stegural of normal type occurs. Since PU1 and U1 are still separate in *Opisthoproctus* (and possibly also in *Macropinna*) it is likely that all early argentinoids had these centra separate, and were also more primitive than *Gaudryella* and *Humbertia* in this feature.

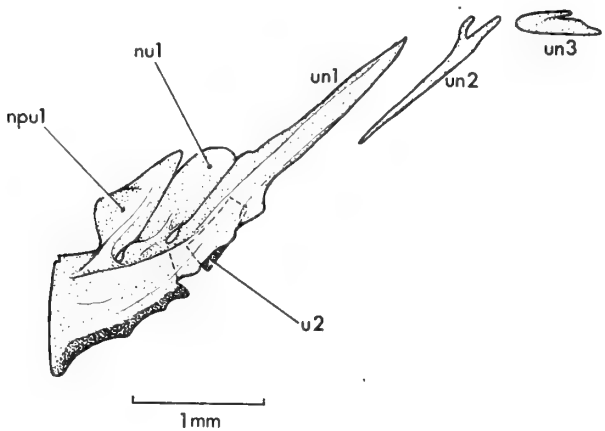

FIG. 41. *Bathylagus antarcticus* Günther, Recent. Dissociated parts of the caudal skeleton of a stained and macerated individual, same specimen as Fig. 37A. Explanation of abbreviations p. 296.

In the osmeroids and stomiatoids the caudal skeleton is similar. In osmeroids it has been illustrated in *Osmerus* (Berg 1955, fig. 198), *Thaleichthys* (Chapman 1941, fig. 15), *Hypomesus* (Gosline 1960, fig. 5), *Spirinchus* (Weitzman 1967b, fig. 4) and *Plecoglossus* (Gosline 1960, fig. 12). *Osmerus* and *Hypomesus* are illustrated here (Figs. 42, 43). All have no free second ural centrum, the parhypural and six autogenous hypurals articulating with a single upturned centrum, and the stegural is fused with this centrum (pu1 + u1 + u2 + st). The stegural has a deep notch in its anterior margin, marking the cleft between the neural arch and uroneural components, as in *Gaudryella* and *Humbertia*. All osmeroids have two epurals, as in argentinoids and *Gaudryella* (the dried skeleton of *Hypomesus* illustrated by Gosline

has two epurals, not one as shown), and there are independent second and third uroneurals (un2, un3), as in *Humbertia*. There is a urodermal in *Osmerus* (Patterson 1968a : 230 ; Fig. 42) and *Hypomesus* (Fig. 43), but caudal scutes are absent (Weitzman 1967b : 532). The neural spine of PU2 is short, as in *Gaudryella* and *Humbertia*, in all published illustrations of osmeroid tails (Gosline's individual of *Hypomesus* is abnormal in having two neural spines, one long and one short, on PU2 ; cf. Fig. 43). In *Osmerus*, Berg illustrates short neural spines on both PU2 and PU3, a most unusual condition, while in the three dried skeletons of *O. eperlanus* available to me, one (npu2, Fig. 42) has a short neural spine on PU2 and the other two have full neural spines. In general, osmeroids show a combination of primitive features (NPU2 short, three uroneurals, hypurals autogenous) and advanced features (no free U2, stegural fused with compound centrum and with no extension forward to PU2, two epurals, no caudal scutes) which distinguish them from both *Gaudryella* and *Humbertia*, but a *Humbertia*-like caudal skeleton could well be antecedent to the osmeroid type.

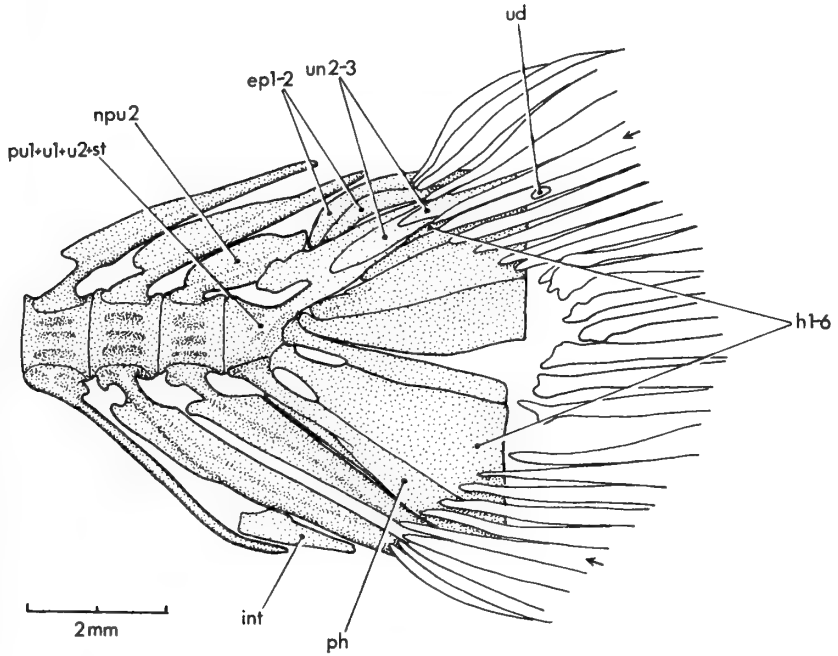

FIG. 42. *Osmerus eperlanus* (L.), Recent. Caudal skeleton of a dried skeleton, BM(NH) unreg., 100 mm., Berlin. Arrows mark the outermost (unbranched) principal fin-rays, explanation of abbreviations p. 296.

In stomiatoids, which Weitzman places as the closest relatives of osmeroids, the caudal skeleton is known in *Polymetme*, *Vinciguerria* (Weitzman 1967b, figs. 15, 10), *Gonostoma*, *Maurolicus* (Monod 1968, figs. 393, 394 ; Weitzman 1967a, fig. 31), *Photichthys* (Gosline 1960, fig. 9) (all Gonostomatidae, the most primitive family according to Weitzman), *Astronesthes*, *Borostomias* (Weitzman 1967a, figs. 14, 31 ;

both Astronesthidae), *Chauliodus* (Monod 1968, fig. 396 ; Chauliodontidae) and *Idiacanthus* (Beebe 1934, figs. 74, 78 ; Idiacanthidae). A free second ural centrum is present in *Polymetme*, *Borostomias antarcticus* and possibly in *Maurolicus*, and in this the stomiatoids are more primitive than osmeroids. In *Polymetme* and *Gonostoma* there are six autogenous hypurals, but in other forms there may be only five (*Photichthys*, astronesthids, *Chauliodus*) or there are various fusions. In *Maurolicus* and *Vinciguerria* hypurals 1 + 2 and 3 + 4 are fused, and there are two slender, autogenous hypurals above, as in *Gaudryella*, while *Vinciguerria* has these two hypural plates and the parhypural fused with the compound centrum. *Borostomias*, *Polymetme* and *Photichthys* have an autogenous stegural of typical shape, but the stegural is fused with the centrum in other genera. There is a second uroneural

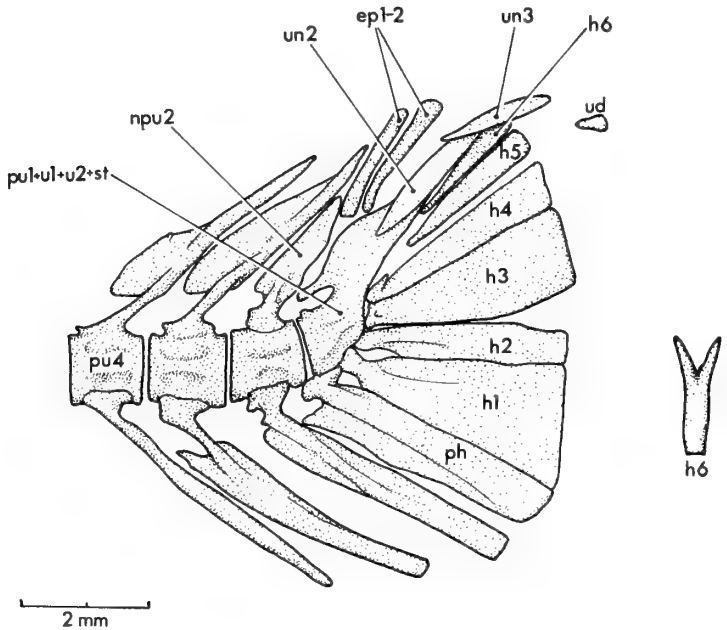

FIG. 43. *Hypomesus olidus* (Pallas), Recent. Caudal skeleton of a stained and macerated individual, same specimen as Fig. 29B. On the right is the detached sixth hypural in dorsal view. Explanation of abbreviations p. 296.

in all genera except *Polymetme* and *Chauliodus*, but none has a third. There are three epurals in *Gonostoma*, two or one in other genera. All stomiatoids have a full neural spine on PU2, and in this they are more advanced than osmeroids, *Gaudryella* and *Humbertia*. No stomiatoid is known to have caudal scutes or a urodermal. There is clearly a wide range of caudal structure in stomiatoids, and no one genus can be clearly characterised as more primitive than the others. The occurrence of a second ural centrum, an autogenous stegural and three epurals in some forms shows that the stomiatoid caudal skeleton cannot be derived from the osmeroid type.

Fusions between the hypurals and centra in some stomiatoids are similar to those in *Gaudryella*, but the tail of *Gaudryella* is more primitive in several ways and any direct relationship is unlikely. As in the osmeroids, however, a *Humbertia*-like caudal skeleton could be antecedent to that of stomiatoids.

Among galaxioids, the caudal skeleton has been illustrated in *Galaxias* (Gosline 1960, fig. 11 ; McDowall 1969, fig. 4B), *Brachygalaxias* (Greenwood *et al.* 1966, fig. 4C) (both Galaxiidae), *Aplochiton* (Chapman 1944, fig. 10 ; McDowall 1969, fig. 4C), *Lovettia* (McDowall 1969, fig. 4D) (both Aplochitonidae *sensu* McDowall), *Prototroctes* (McDowall 1969, fig. 4E ; Prototroctidae), and *Retropinna* (McDowall 1969, fig. 4A; Retropinnidae). *Galaxias brevipinnis* is illustrated here (Fig. 44).

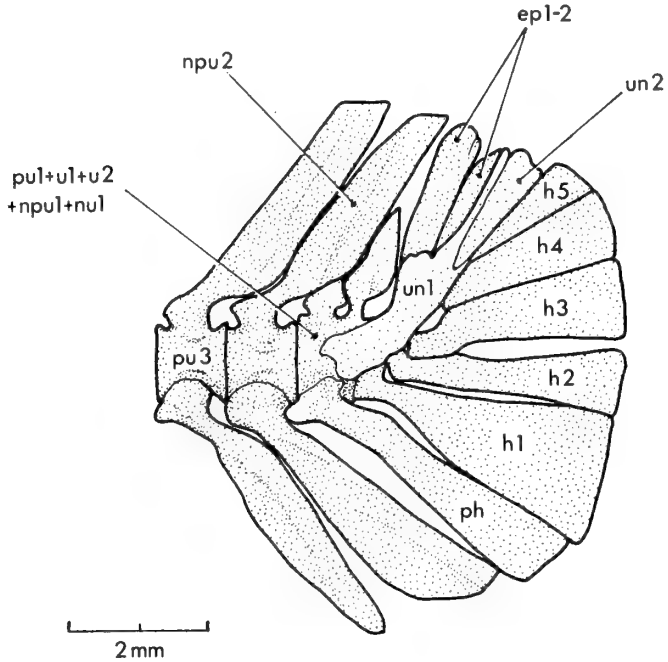

FIG. 44. *Galaxias brevipinnis* Günther, Recent. Caudal skeleton of a dried skeleton, BM(NH) unreg., 105 mm., New Zealand. Explanation of abbreviations p. 296.

McDowall has recently (1969) made an osteological investigation of the galaxioids and finds that they fall into two groups (at present unnamed), one containing the Retropinnidae and Prototroctidae, the other the Galaxiidae and Aplochitonidae. This separation is shown very clearly by the structure of the caudal skeleton. In *Retropinna* and *Prototroctes* (dried skeletons of *Prototroctes oxyrhynchus* and *Retropinna* sp. examined) the caudal skeleton is similar, with six hypurals, the four upper ones autogenous, the two lower ones more or less fused with the parhypural (cf. *Gaudryella*), a low, broad neural spine on PU2 (as in *Gaudryella*, *Humbertia* and most osmeroids), three epurals, a large stegural with a deep notch in

its anterior margin (again as in *Gaudryella*, *Humbertia* and osmeroids), a second uroneural, and 16 branched caudal rays. In some populations of *R. retropinna* McDowall reports a small second ural centrum, but in most *Retropinna* and in *Prototroctes* there is no U2. The stegural appears to be autogenous in the dried skeletons I have examined and in McDowall's figures, but in *Retropinna* he describes it as ' more or less ankylosed ' to the compound centrum. This caudal skeleton is strikingly like those of the osmeroids, differing only in the partial fusion of the parhypural and the lower hypurals, the three epurals, the absence of a third uroneural, and the autogenous stegural, all features which occur in the stomiatoids. The caudal skeletons of *Retropinna* and *Prototroctes* are also very like that of *Gaudryella*.

The galaxiids and aplochitonids have only five hypurals, a neural spine on PU2 which is often double but usually (? always) complete, two or less epurals, two uroneurals of which the first is autogenous in Gosline's and McDowall's specimens (see also Fig. 44), but is fused with the centrum in the BM(NH) dried skeletons of *Galaxias platei* and *Aplochiton zebra*, and 14 or less branched caudal rays. In *Brachygalaxias* there is a second ural centrum. A most important feature of all galaxiids and aplochitonids is the presence of one or two neural arches with variously developed neural spines on the compound centrum. These neural arches are often fused with the underlying centrum (Fig. 44) but are quite distinct from the first uroneural. The galaxiids and aplochitonids appear never to have developed a stegural, the neural arches of PU1 and U1 fusing with the centrum, not the uroneural, as in argentinoids (see above). This would exclude them from close relationship with *Gaudryella* and *Humbertia*, and whereas the caudal skeletons of *Prototroctes* and *Retropinna* resemble those of the osmeroids, stomiatoids, *Gaudryella* and *Humbertia*, those of galaxiids and aplochitonids resemble those of argentinoids (cf. Figs. 38–41, 44). These differences suggest that the galaxiid-aplochitonid assemblage and the retropinnid-prototroctid assemblage may not be so closely related as is generally assumed.

In primitive euteleostean fishes it seems that there are two alternative methods of incorporating the neural arches of the first pre-ural and ural centra. The first method is to fuse the paired halves of these arches with the first uroneurals, which acquire dorso-medially directed flanges and become typical segurals : there is then no sign of arches on the underlying centrum. The 'type ' stegural is that of the salmonids (see illustrations in Norden 1961 ; Vladykov 1962 ; Monod 1968). A similar stegural occurs in esocoids, osmeroids, stomiatoids, prototroctids, retropinnids, and the neoteleosts. The second method is for the neural arches of PU1 and U1 to remain separate or to fuse with the underlying centrum, the first uroneural being unmodified. This is characteristic of the alepocephaloids (including the Bathylaconoidei, Nielsen & Larsen 1968 ; Gosline 1969), argentinoids, galaxiids and aplochitonids.

In gonorynchiforms and ostariophysans, the only euteleosteans not yet mentioned, the caudal skeleton is greatly simplified by fusion, even in the most primitive forms (*Chanos*, Monod 1968, fig. 113 ; the Cretaceous gonorynchid *Charitosomus*, Fig. 45 ; and various ostariophysans illustrated by Monod 1968). But the configuration of

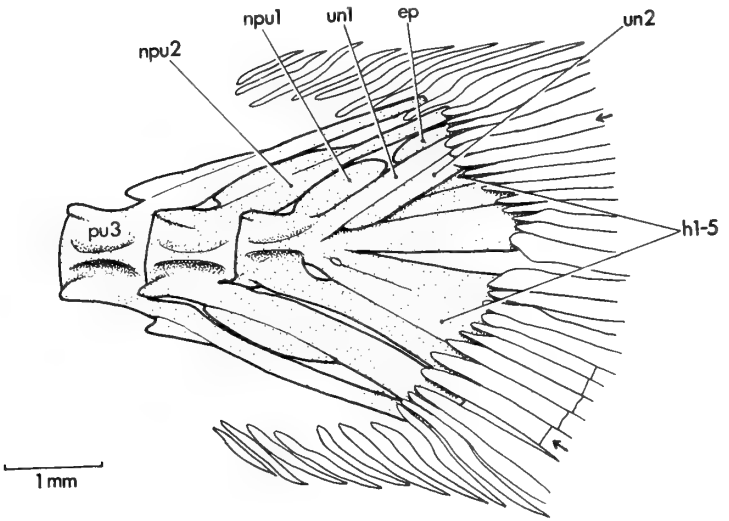

FIG. 45. *Charitosomus hakelensis* Davis, Middle Cenomanian, Hakel, Lebanon. Restoration of caudal skeleton based on P.13897. Arrows mark the outermost (ubranched) principal fin-rays, explanation of abbreviations p. 296.

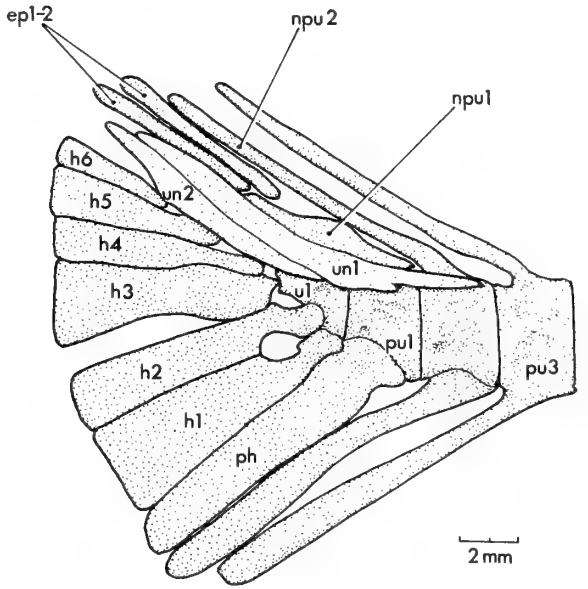

FIG. 46. *Tharrhias araripis* Jordan & Branner, Santana Formation (? Albian), Serra do Araripe, Brazil. Restoration of caudal skeleton based on specimens in a private collection. Explanation of abbreviations p. 296.

the element labelled ' ANP1 ' by Monod in *Gonorynchus* and ostariophysans (see especially figs. 465, 468–470) is such that I agree with Monod that it is a neural arch, not part of a stegural. In the specimen of *Chanos* illustrated by Monod this element is very small, but in each of five small individuals that I have examined it is much as in *Charitosomus* (npu1, Fig. 45). Since this element is fused with the compound centrum in all ostariophysans, as is the first uroneural, it is impossible to be certain of its homologies. There are several Lower Cretaceous genera which are supposed to be relatives of *Chanos* (*Prochanos, Parachanos, Chanopsis, Dastilbe, Tharrhias* ; Santos & Valenca 1968). Amongst these, the caudal skeleton is known in *Parachanos* (Arambourg & Schneegans 1936, fig. 5), *Dastilbe* (Santos 1947, figs. 5, 6) and *Tharrhias* (Fig. 46). In all these it is very similar, with PU1 and U1 separate, six autogenous hypurals, a full neural spine on PU2, two (or less) epurals, and two uroneurals, the first of which extends forwards across PU2. Probably, all have a small U2, hidden below the second uroneural (U2 is visible in one specimen of *Dastilbe* where the second uroneural is displaced). Between the first uroneurals and above PU1 and U1 there is a separate, elongate bone (labelled ' na ' by Arambourg & Schneegans ; npu1 in Fig. 46) which must represent the neural arch of PU1 (cf. *Albula*, Monod 1968, figs. 96–103). If these Lower Cretaceous fossils are really relatives of *Chanos* (which is not possible to prove at present, but is likely because of the structure of the jaws and cheek, the enlarged first rib, and other features) separation of the first uroneural and the neural arch of PU1 is further evidence that the gonorynchiforms and ostariophysans never developed a stegural, and provisionally they can be included with the other euteleosteans of this type.

Fig. 47 is modified from Gosline's (1960) diagram 2, incorporating information from the caudal skeleton only. Whether this is a valid scheme is debatable, but at least it offers some testable hypotheses. On present evidence, *Gaudryella* and *Humbertia* fall with the osmeroids, stomiatoids and retropinnids, as shown.

(v) *Conclusions*

Despite many resemblances to the argentinoids, both general (p. 254) and particular (reduced dentition, long vomer, ethmoid of *Humbertia*, premaxilla of *Gaudryella*, etc.) any close relationship between *Gaudryella* or *Humbertia* and the argentinoids is excluded by the cellular skeleton, absence of a true stegural, and occasional presence of separate PU1 and U1 in argentinoids (Fig. 47). Although *Humbertia* is more similar to the argentinoids than is *Gaudryella* in the ethmoid, mandibular dentition and branchiostegals, *Gaudryella* is more argentinoid-like than *Humbertia* in the toothless premaxilla, reduced metapterygoid and toothed basihyal, so that it cannot be said that either genus is closer to the argentinoids than the other. Many of the resemblances between argentinoids and the fossil genera are in primitive characters. Others, especially those in the jaws, vomer, and dentition must be regarded as parallelisms.

There is not much resemblance between either *Gaudryella* or *Humbertia* and the galaxioids (*Retropinna* and *Prototroctes* excluded), and, as in argentinioids, any close relationship is excluded by the absence of a stegural in galaxioids (Fig. 47).

As possible relatives of *Gaudryella* and *Humbertia* there remain only the osmeroids,

stomiatoids and the ' galaxioids ' *Retropinna* and *Prototroctes*. Such a relationship is opposed by the long vomer and lack of endopterygoid teeth in *Gaudryella* and *Humbertia*, by the toothless premaxilla and reduced metapterygoid of *Gaudryella* and the sutured ceratohyal and toothless basihyal of *Humbertia*. But in almost every other character the differences between these living groups and the fossil genera are due to the retention of primitive characters in the latter. The best positive evidence for such a relationship is provided by the structure of the caudal skeleton.

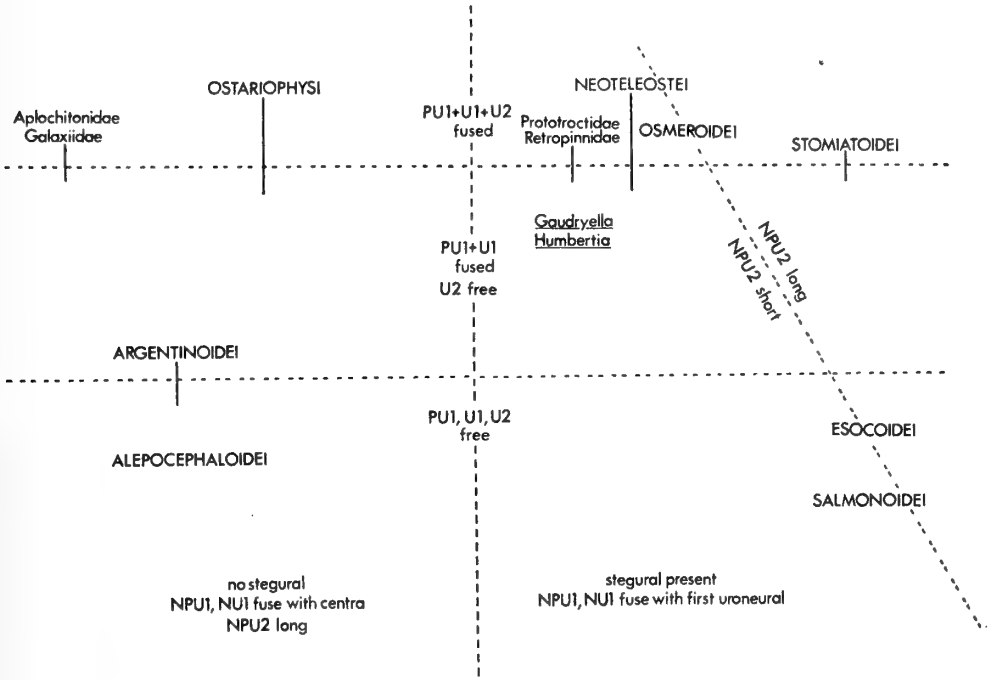

FIG. 47. Diagram showing the distribution of certain caudal structures in euteleosteans. The solid line below certain groups indicates that some members exhibit the more primitive grade of structure. For further explanation see text.

Weitzman (1967b : 533) has constructed an archetype which could be the common ancestor of living osmerids and stomiatoids. This hypothetical proto-osmerid resembles *Gaudryella* and *Humbertia* in many ways, although the two fossil genera are more primitive in having an orbitosphenoid, a fully roofed post-temporal fossa, and various other features not listed by Weitzman. The major differences between the fossil genera and Weitzman's archetype, apart from those in the dentition, concern the ethmoid region, the shape of the palatine, and the lower jaw. The structure of these in Weitzman's archetype seems to be strongly influenced by the opinion, originating with Chapman (1941) and endorsed by McAllister (1963, 1966), that *Spirinchus* and/or *Thaleichthys* are the most primitive osmerids. The reasoning on

which these opinions are based seems to me suspect. Chapman (1941 : 297) decided that *Thaleichthys* was the most primitive osmerid because of the large amount of cartilage in the preorbital part of the braincase, the numerous ethmoid bones, and the development of membranous wings linking the pterosphenoid and prootic. In my opinion, all these are advanced characters, those of the neurocranium because of reasons given in the discussion of the ethmoid region above, those of the pterosphenoid and prootic because they involve the development of membrane bone outgrowths from primitively endochondral bones. McAllister (1963) followed Chapman in regarding *Thaleichthys* as the most primitive osmerid, but recognised two subfamilies, Hypomesinae and Osmerinae, which must be of equal age, as his dendrogram (fig. 13) shows. But in 1966 McAllister published a numerical study of osmerids based on the information in his earlier conventional study, and produced a new dendrogram (1966, fig. 2) which placed *Thaleichthys* as the most primitive osmerid, below the common ancestry of Hypomesinae and Osmerinae, with *Spirinchus* as an advanced member of the Osmerinae. This reversal of the positions of *Spirinchus* and *Thaleichthys* was arrived at partly by counting the primitive characters found in each osmerid genus, and partly by computing the coefficient of association between Hypomesinae and each osmerine genus ; only the first of these procedures will be commented on here. McAllister cited 22 osmerid character states which he considered primitive. The primitive condition of each character was discovered by making two assumptions, first, that paired proethmoids are primitive, and second that salmonines are close to the ancestry of osmerids, and that characters shared by salmonines and any osmerid are therefore primitive. Neither of these assumptions is justified in my opinion. The first is discussed above (p. 259). The second leads McAllister to find that the medioparietal skull roof of *Hypomesus* is a derived condition, and that primitive osmerid characters include such things as caniniform basihyal teeth and approximately three scale rows per trunk segment (as in *Mallotus*, all other osmerids having approximately one scale row per segment). Some of the character pairs selected by McAllister for his ' primitiveness ' count are such that I believe no decision is possible on which state is the more primitive (angle of mouth, place of spawning, adult size). But Chapman (1941) mentions osteological features of certain osmerid genera which can confidently be characterised as primitive, such as the anterior strut on the intercalar in Hypomesinae and *Spirinchus*, the absence of a membrane bone strut between the pterosphenoid and prootic in Hypomesinae, and the slender palatine of Hypomesinae (cf. Fig. 22B). These, and other characters suggest to me that Hypomesinae are the plesiomorph sister-group of Osmerinae, and that *Hypomesus* is the most primitive osmerid genus. Further evidence of this is provided by the almost semicircular operculum of *Hypomesus* (cf. Weitzman 1967b : 529), the small, anteriorly placed recess on the inner face of the dentary (p. 267, Fig. 37B) and the autogenous parapophyses and neural arches on the anterior vertebrae (fused with the centra in other osmerids according to Weitzman (1967b : 530)). Indeed, it seems that many of the similarities between osmerids and stomiatoids on which Weitzman (1967b) places emphasis are in fact similarities between stomiatoids and Osmerinae. This at least raises the possibility that the shallow mandible, long jaws, large gape and short ventral limb of the preopercular in

osmerines and stomiatoids are not primitive for the group. The very long jaws, caniniform teeth and posteriorly inclined, almost palaeoniscoid suspensorium of many stomiatoids are surely secondarily acquired, and one could argue that the vertical suspensorium, moderately long jaws and relatively large teeth of osmerines represent the beginning of a trend towards enlargement of the jaws and teeth from a *Hypomesus*-like (or *Humbertia*-like) ancestor. Such changes in the jaws might be correlated with changes in jaw mechanics associated with the development of a posteriorly placed recess housing the insertion of the adductor mandibulae in the dentary. One is accustomed to regard the triangular mandible and villiform teeth of such fishes as *Elops, Aulopus* and *Polymixia* as the primitive condition in all teleostean lineages (cf. Gosline 1959), and to think of shortening of the gape and deepening of the mandible as irreversible changes. But a small mouth and deep mandible of the type found in *Hypomesus, Gaudryella* and *Humbertia* are so widely distributed among primitive teleosts (p. 266) that it is tempting to see this arrangement as a necessary consequence of the jaw mechanics of primitive forms, and as being reversible in lines where some new modification of jaw mechanics occurs.

It is therefore not entirely unreasonable to regard the *Hypomesus*-like jaws of *Gaudryella* and *Humbertia* as proto-osmerid characters, and to place these fishes near the line leading to osmeroids. Precisely where *Plecoglossus* and the salangids stand in this grouping, I cannot say, but I agree with McDowall (1969 : 816, 821) that these fishes are closer to the osmerids than to any other group, and should be included in the Osmeroidei. *Plecoglossus* and the salangid available (*Leucosoma*, cf. Gosline 1960 : 339) have caudal skeletons which are entirely of osmerid type, although *Leucosoma* exhibits considerable fusion within the lower and upper hypurals, much as in *Gaudryella* (see Nelson 1970 for another view of salangid relationships). *Retropinna* and *Prototroctes* present another problem because of their southern distribution, because of certain resemblances to the galaxioids, and because their caudal skeletons are more primitive than those of osmerids in having the stegural autogenous, a second ural centrum in some, and three epurals (all characters found in stomiatoids). They have a short vomer, a low mandible of osmerine type and the osmerid cucumber smell, but no supramaxilla, no mesocoracoid and the palatine and ectopterygoid fused. I would suggest, tentatively, that they be placed in the Osmeroidei.

In summary, the only group of living fishes with which either *Gaudryella* or *Humbertia* can be aligned is that salmoniform subgroup containing the Osmeroidei (and Stomiatoidei, if Weitzman is correct). This is hardly a satisfactory solution, for *Gaudryella* and *Humbertia* are far more primitive than any member of these groups and one cannot help being impressed by various argentinoid-like features which prevent either genus from being very close to the hypothetical proto-osmerid, the common ancestor of the group. But there are strong objections to any other solution.

There remains the problem of the interrelationships of *Gaudryella* and *Humbertia* (the size of the 'gap' between them). The differences between the two genera (Table 3) are such that if they were living fishes one would hardly place them in the same family, and the significance of these differences is increased by the age of the fossils, for in middle Cretaceous times the differences between what are now sharply distinct

groups were small (e.g. myctophiforms, paracanthopterygians and acanthopterygians ; Rosen & Patterson 1969). But I can find no convincing evidence that either genus is closer to any living group than the other, and have no reason to separate them on these grounds. Among fishes contemporary with *Gaudryella* and *Humbertia*, where most comparisons are admittedly useless because of lack of information on other forms, the same conclusion is reached (see below), and despite the trenchant differences between *Gaudryella* and *Humbertia* I am forced to regard them as each other's closest known relatives. Under these circumstances, the erection of a monotypic family for each genus would be meaningless, especially since there exists no named higher taxon (except Salmoniformes) in which to place them.

The superorder Protacanthopterygii of Greenwood *et al.* (1966) has been shrinking rapidly as various component groups are hived off into other taxa. With the removal of the myctophoids, ctenothrissiforms, and most of the cetomimiforms to the Neoteleostei (McAllister 1968 ; Rosen & Patterson 1969) and the removal of the gonorynchiforms to the Ostariophysi (Rosen & Greenwood 1970), the superorder Protacanthopterygii is now an ' empty category ', containing only the order Salmoniformes (including the Giganturoidei, Rosen & Patterson 1969 : 455). Rosen & Greenwood removed the gonorynchiforms from the Protacanthopterygii because they felt that the group would otherwise be paraphyletic. But even after these fishes have gone, there is almost no evidence that the remaining protacanthopterygian group, the Salmoniformes, is monophyletic (absence of ectopterygoid teeth seems the only advanced character common to all salmoniforms). Despite recent detailed anatomical work on four of the eight salmoniform suborders (osmeroids and stomiatoids, Weitzman 1967a, b ; alepocephaloids, Gosline 1969 ; galaxioids, McDowall 1969) there is still no coherent picture of relationships among these groups. Not even Weitzman's demonstration of osmeroid-stomiatoid relationships can be regarded as well founded (Nelson 1970), and we are no nearer an understanding of the closest relatives of, for example, the salmonoids, esocoids or argentinoids. Discussions of salmoniform interrelationships by Gosline (1969) and McDowall (1969) suggest that at this level we have run out of characters on which to sort out these groups. The present investigation has produced nothing new in the skull which might be useful here, but there is one feature of the caudal skeleton which seems promising, the fate of the neural arches of the first pre-ural and ural centra. This character (Fig. 47) suggests that salmoniforms might fall into two groups, the first containing alepocephaloids, argentinoids and galaxioids (less prototroctids and retropinnids), the second containing salmonoids, esocoids, osmeroids and stomiatoids (I can find no information on these structures in giganturoids). Goody (1969) has erected four extinct salmoniform suborders containing rather specialised Cretaceous fishes : of these, the Ichthyotringoidei fall in the first group (Goody 1969, fig. 4), the Enchodontoidei and probably also the Halecoidei fall in the second (Goody 1969, figs. 42, 48, 64, 69), and information is lacking on the caudal skeleton of Cimolichthyoidei.

Such a division correlates rather well with the development of the neural spine of the second pre-ural centrum, which is long in all members of the first group, short in various representatives of all suborders except stomiatoids in the second. A further consequence of a division along these lines would be that the first group is related to

the ostariophysans, the second to the neoteleosts, each group containing a primitive basal suborder (alepocephaloids in the first, salmonoids in the second) and a series of more advanced groups foreshadowing or paralleling the major radiations of the ostariophysans and neoteleosts. In the ostariophysans and neoteleosts, however, correlation with the development of the neural spine of PU2 is not perfect, for although a short neural spine is characteristic of primitive neoteleosts, it is also found quite frequently in ostariophysans (*s.str.*), apparently as an individual variation (cf. Monod 1968, figs. 456–521). Should future investigations support such a division of the Euteleostei, it may be possible to do away with the Protacanthopterygii (or to reserve this name for the salmonoid-osmeroid group).

(c) Comparisons with *CLUPAVUS* and the CLUPAVIDAE

The genus *Clupavus* was erected by Arambourg (1950 : 417) for a group of uppermost Jurassic (Purbeckian) and Cretaceous species of *Leptolepis* similar to the Purbeckian *L. brodiei* Agassiz, selected as type-species. *Clupavus* was said to be intermediate between *Leptolepis* and the Dussumieriinae. In 1955 (p. 33) Arambourg placed *Clupavus* in the Clupeidae and listed ten species of the genus in addition to *C. brodiei* (but including *Leptolepis valdensis* Smith Woodward, previously transferred to *Anaethalion* by Smith Woodward (1919 : 126)). In the *Traité de Zoologie*, Bertin & Arambourg (1958 : 2230) erected the family Clupavidae, with *Clupavus* as the only contained genus, which they placed in the Clupeoidei, commenting further on its relationship to leptolepids and clupeoids.

Recently (1968) Arambourg has published a ' rectification de nomenclature ' on *Clupavus*, stating that he now recognises *Leptolepis brodiei* as a true *Leptolepis*, and (" afin d'éviter toute discussion byzantine ultérieure ") replacing it as type-species of *Clupavus* by *C. maroccanus* Arambourg (1968), a species based on material from the Lower Cenomanian of Morocco which was previously (1955) described as *Clupavus* cf. *neocomiensis* Bassani. I have examined the type material of *L. brodiei* and I agree with Arambourg that the fish shows nothing to distinguish it from *Leptolepis s.l.* Arambourg's emendation of the type-species of *Clupavus* will have to be ratified by the International Commission (Article 70 of the ' Code '), but I accept it here since it clarifies the meaning of *Clupavus*, and since *C. maroccanus* is almost the only species referred to the genus on which any sort of detailed anatomical information is available in the literature.

Clupavus maroccanus is a small fish which is superficially, and in many details of the skull, vertebral column and fins, so like *Gaudryella* and *Humbertia* that in 1967, before recognising the differences between the latter, I confidently assigned the Lebanon fishes to *Clupavus*. Through the kindness of Prof. C. Arambourg and Mlle J. Signeux I have been able to examine some of the type material of *C. maroccanus* from Jebel Tselfat, Morocco. This material is so preserved that it is not possible to elucidate many details of the skull, and no very detailed comparison with *Gaudryella* and *Humbertia* can be made. *C. maroccanus* resembles *Gaudryella* rather than *Humbertia* in the following characters :

1. Trunk relatively compressed, since the fish is frequently preserved in lateral view.

2. Ethmoid strongly ossified and of complex shape.
3. Branchiostegals rather numerous (about 10) and slender.
4. Premaxilla toothless.
5. Subopercular smaller than opercular.
6. Pelvics below 21st or 22nd vertebra.
7. Dorsal originating over 15th vertebra, with 12 rays.
8. Caudal scutes absent or very small.

This list contains a few advanced characters, while the features in which *C. maroccanus* resembles *Humbertia* rather than *Gaudryella* seem to be all primitive (parietal branch of supraorbital canal large ; head of hyomandibular single ; metapterygoid large). There is some evidence here that *Clupavus* is closer to *Gaudryella* than *Humbertia*, but in the apparent absence of teeth on any bone, *C. maroccanus* differs from both *Gaudryella* and *Humbertia*.

The most valuable evidence comes from the caudal skeleton. *C. maroccanus* has the first pre-ural and ural centra fused, like *Gaudryella* and *Humbertia*, and is therefore probably a euteleostean, not a clupeomorph (this is also indicated by the well developed articular head of the first hypural, which is absent or reduced in clupeomorphs). Several potentially important features of the caudal skeleton cannot be seen in *C. maroccanus* (presence or absence of a second ural centrum, a urodermal and a third uroneural, number of epurals, etc.), but there are three characters which distinguish it from *Gaudryella* and *Humbertia* : first, the first uroneural does not extend on to the second pre-ural centrum ; second, there is a complete neural spine on the second pre-ural centrum, and this is a constant feature of the species, just as the short neural spine is constant in *Gaudryella* and *Humbertia* ; third, there appears to be a short neural arch on PU1 + U1, which is separate from the first uroneural, much as in *Argentina* (npu1, Fig. 38). These last two characters would place *Clupavus* on the left hand side of the diagram in Fig. 47, suggesting that it may be related to the argentinoids, but can hardly be close to *Gaudryella* or *Humbertia*. For these reasons, neither *Gaudryella* nor *Humbertia* can be included in the Clupavidae.

Other species which have been referred to the Clupavidae by Arambourg and subsequent workers are listed below, with brief notes on their significance.

Leptolepis formosus Traquair, *L. attenuatus* Traquair, *L. brevis* Traquair. These three species are from the Wealden (continental lowermost Cretaceous) of Bernissart, Belgium (Traquair 1911). None has been redescribed since Traquair's work, and the holotypes of *L. formosus* and *L. attenuatus* are now lost. From the published descriptions one can learn nothing of value in deciding on their status, but from their age it is unlikely that they can have much to do with *Clupavus*, *Gaudryella* or *Humbertia*.

Leptolepis neocomiensis Bassani, *L. neumayri* Bassani, *L. checchiai* d'Erasmo, *L.* aff. *voithi* Agassiz. These four species are from Albo-Aptian (Pietraroia, Castellammare) and Cenomanian (Lesina, Comen and neighbouring localities) deposits in Italy and Jugoslavia.

L. neumayri (Bassani 1882 : 14), from the Lower Cenomanian of Lesina and Comen, was transferred to the myctophoid genus *Leptosomus* (= *Cassandra*, a

synonym of *Sardinioides* according to Goody 1969) by d'Erasmo (1964 : 103) and this is certainly correct.

L. neocomiensis, which has often been synonymised with *L. brodiei* Agassiz, is recorded at Pietraroia (d'Erasmo 1915, as *L. brodiei*), Castellammare (Bassani & d'Erasmo 1912, as *L. brodiei*), Lesina (Bassani 1882) and Comen (d'Erasmo 1946). The species is superficially similar to *Clupavus maroccanus*, for Arambourg at first described the latter as *C.* cf. *neocomiensis*. Between the four populations of *L. neocomiensis* cited above (that from Castellammare described on only two specimens), there is considerable variation in meristic characters (proportions, fin-ray and vertebral counts), and apart from these features there is very little in the descriptions on which comparisons can be based. The BM(NH) contains one specimen from Castellammare (P.3612), cited by Bassani & d'Erasmo (1912 : 230), which agrees well enough with their description of *L. brodiei*. This specimen is poorly preserved and yields no detailed information in the skull. But there are epipleurals in the middle part of the trunk, suggesting that it is not a *Leptolepis* (which has epineurals only), while the neural spine of PU2 is short and there are large caudal scutes, distinguishing it from *Clupavus*. These two characters of the tail are primitive features also present in *Humbertia*, but there is no information regarding most of the characters in which *Humbertia* differs from *Gaudryella* and no means of telling whether it resembles one of these genera more than the other.

The BM(NH) also contains two specimens from Comen (P.10617–8) which agree with the population of *L. neocomiensis* described from there by d'Erasmo (1946). These fishes are fairly well preserved, though bituminised, and the caudal skeleton (Fig. 48) shows a short neural spine on PU2, a stegural of normal form, three epurals, PU1 and U1 fused, and the characteristic salmoniform expansions on the last few neural and haemal spines. The last two characters show that it is a euteleostean fish, and the neural spine of PU2 and the stegural distinguish it from *Clupavus*. This caudal skeleton is rather like those of *Gaudryella* and *Humbertia*, though the preservation is not good enough for detailed comparisons, but the fish is easily distinguished from them by the smaller vertebral number and more numerous caudal vertebrae (34 vertebrae, 16–17 caudals ; d'Erasmo gives 32–36, c. 18 caudal), by having only 9 pelvic rays, and by the deeper trunk (depth about 25% standard length). In the skull, the lower limb of the preopercular is much shorter than in *Gaudryella* and *Humbertia*, there is a robust, toothless premaxilla, a long, slightly curved maxilla which extends back to the quadrate and bears rather large teeth, a heavily ornamented posterior supramaxilla, and a short series of rather large teeth on the lower jaw.

L. aff. *voithi* Agassiz, described from Castellammare by Bassani & d'Erasmo (1912 : 231) on the basis of five specimens, is similar to *Clupavus*, *Gaudryella* and *Humbertia* in proportions, fin positions and vertebral number (40 vertebrae, 15 caudal), but has a larger dorsal fin (16 rays). From the published description there is no evidence to suggest that it is closer to one of these genera than to the others.

L. checchiai d'Erasmo (1946 : 37), described on the basis of ten specimens from Comen, appears to have PU1 and U1 fused and has a large subopercular and 36–38 vertebrae, resembling *Humbertia* rather than *Clupavus* or *Gaudryella*, but there is a

complete neural spine on PU2 (d'Erasmo 1946, fig. 13C) and the anal fin lies well forward, closer to the pelvics than to the caudal. Once again, there is no means of deciding on the relationships of this species.

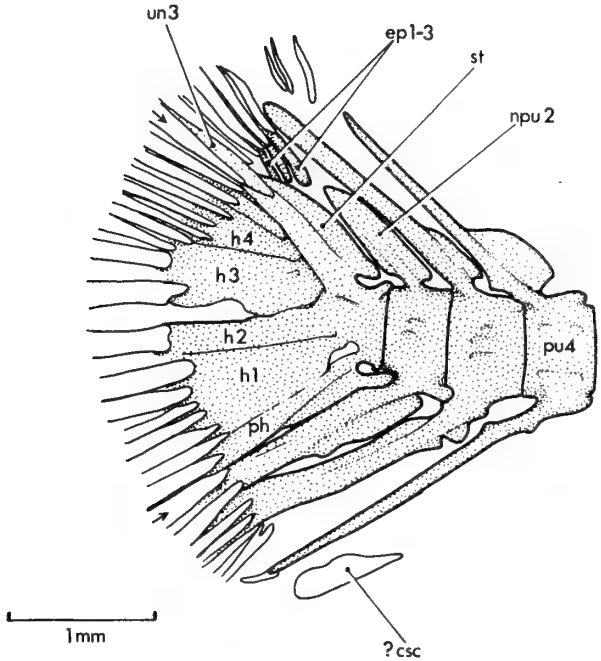

FIG. 48. '*Leptolepis*' *neocomiensis* Bassani, Lower Cenomanian, Comen, Jugoslavia. Caudal skeleton as preserved in P.10617. Arrows mark the outermost (unbranched) principal fin-rays, explanation of abbreviations p. 296.

Leptolepis congolensis Arambourg & Schneegans (1936 : 13) is from the Cocobeach series of Angola. These continental beds have recently been placed in the Wealden on the evidence of ostracods (Grekoff & Krömmelbein 1967). *L. congolensis* is superficially similar to *Clupavus*, *Gaudryella* and *Humbertia*, but has a deeper trunk (c. 25% of the standard length) and the pelvics are inserted below the origin of the dorsal. The subopercular is large, teeth are few or absent and no epipleurals have been seen. Arambourg & Schneegans' drawing of the caudal skeleton (1936, fig. 8) is schematic, but it shows PU1 and U1 fused, a short neural spine on PU2, and large caudal scutes. The last two characters distinguish it from *Clupavus* and the large caudal scutes suggest that it is not close to *Gaudryella*. Further information is necessary before anything positive can be said about its relationships.

Clupavus yamangiensis Casier and *C. longicaudatus* Casier are from early Cretaceous deposits in the Congo (Casier 1961 : 54, 57). Each is based on a single defective specimen and very little is known of them. *C. yamangiensis* is described as having no teeth, no large coronoid process on the dentary, a very short dorsal fin and

the pelvic and anal fins further forwards than they are in *Clupavus*, *Gaudryella* and *Humbertia*. In the caudal skeleton (N. Bonde, personal communication) PU1 and U1 appear to be fused and there is a full neural spine on PU2 and a shorter neural spine on PU1, the last two characters suggesting relationship with *Clupavus*. There are only eighteen principal caudal rays, which would distinguish the species from all others under consideration here.

C. longicaudatus is said by Casier to have 25 or less vertebrae, many fewer than any other supposed clupavid. But the single specimen is badly distorted and no diagnostic characters are preserved (N. Bonde, personal communication).

Paraclupavus caheni Saint-Seine & Casier (1962 : 30) is from the Kimmeridgian (Upper Jurassic) of Songa, Congo. It is a primitive form, with three supraorbitals, a large basipterygoid process, long parietals, very large post-temporals, and 17–18 branchiostegal rays. Although three series of intermuscular bones are mentioned in the original description, N. Bonde (personal communication) finds that there are epineurals only, as in leptolepids, that PU1 and U1 are separate, and that each bears a small neural arch. *Paraclupavus* appears to be a relative of the leptolepids, from which it differs principally in the reduced number of vertebrae (34), the absence of pit-lines or a branch of the supraorbital canal on the parietal, the slender infraorbitals, and the absence of scales.

Leptolepis nevadensis David (1941) is referred to *Clupavus* by Lehman (1966 : 191). This species is based on about a dozen specimens from the Lower Cretaceous Weber Conglomerates of Nevada. It has 49–50 vertebrae (15 caudal), more than any other ' clupavid ', and has epineurals only. No teeth have been seen. In the caudal skeleton (David 1941, fig. 3 ; personal observations) the neural spine of PU2 is complete and there are small neural arches on PU1 and U1 which are distinct from the first uroneural, PU1 and U1 are separate and there are large caudal scutes. Separation of PU1 and U1 distinguish the species from *Clupavus*, *Gaudryella* and *Humbertia* and place it in some more primitive group, but nothing positive can be said about its relationships.

Clupavus casieri Taverne (1969) is based on numerous specimens from the Upper Santonian of Vonso, Congo. The species is said by Traverne to be very similar to *C. maroccanus*. Like the latter it is toothless, but it has only 35–37 vertebrae (less than in *C. maroccanus* or *Gaudryella*) and a rather long anal fin, with fifteen rays, many more than in *C. maroccanus*, *Gaudryella* or *Humbertia*. There appears to be a complete neural spine on PU2, a difference from *Gaudryella* and *Humbertia* and a resemblance to *Clupavus*. Almost nothing is known of the skull or caudal skeleton, and nothing can yet be said on its relationships.

Bonde (1966 : 199) has referred to the Clupavidae an undescribed fish which is common in the Lower Eocene Mo-clay of Denmark. He now believes (personal communication) that this fish cannot be positively referred to the Clupavidae but that it is a primitive salmoniform whose relationships remain to be discovered.

From this survey it is clear that the family Clupavidae, as now constituted, is not a useful taxon. Although all the fishes placed in the family are superficially similar, they are easily distinguished from *Clupavus maroccanus*, the only undoubted clupavid, wherever detailed information is available. Supposed clupavids seem to fall into

three categories. First, and most numerous, are those species which are so poorly preserved or described that nothing is known which might bear on their relationships : *Leptolepis formosus, L. attenuatus, L. brevis, L. neocomiensis* (the population from Comen excepted), *L.* aff. *voithi, Clupavus longicaudatus, C. casieri.* Second, there are two species, *Paraclupavus caheni* and *Leptolepis nevadensis,* which have the first pre-ural and ural centra separate and therefore belong to some more primitive group than that containing *C. maroccanus.* Third, there are four species, *Leptolepis neocomiensis* (population from Comen), *L. checchiai, L. congolensis* and *Clupavus yamangiensis,* which have the first pre-ural and ural centra fused, like *Clupavus, Gaudryella* and *Humbertia.* These four species then fall into two groups, those with a short neural spine on PU2, *L. neocomiensis* and *L. congolensis,* and those with a long neural spine on PU2, *L. checchiai* and *C. yamangiensis* ; only the last two species are probable members of the Clupavidae. All that can be said of the Clupavidae at present is that they appear to be euteleostean fishes, not clupeomorphs, and that the structure of the caudal skeleton in the type-species suggests a possible relationship to the argentinoids. *Leptolepis neocomiensis* and *L. congolensis* are possible relatives of *Gaudryella, Humbertia* or the osmeroids and stomiatoids, but the available information does not allow a decision. *L. congolensis,* because of its Wealden age, may prove to be of particular interest.

(d) Comparison with other Cretaceous teleosts

Bassani (1882 : 31) and Kramberger (1895 : 37) have referred to *Clupea gaudryi* (= *Gaudryella gaudryi*) specimens from the Lower Cenomanian of Lesina, Comen and Mrzlec (near Solkan, Jugoslavia). Bassani's two specimens from Lesina agree with *Gaudryella* rather than *Humbertia* in the position of the dorsal fin (origin over the seventeenth vertebra ; predorsal length c. 45% standard length), the apparently toothless premaxilla (Bassani 1882, pl. 7, fig. 2), small subopercular, and in having 42 vertebrae (but there are said to be 18 caudal vertebrae and only 18 pairs of ribs, while *G. gaudryi* has only 15 caudals and about 26 pairs of ribs). In having 14 dorsal rays the specimens resemble *Humbertia* rather than *Gaudryella.* These fishes differ from both *Gaudryella* and *Humbertia* in having a larger anal fin (11 rays), apparently no epipleurals, and, according to Bassani, traces of abdominal scutes. This last character may well be an error, for similar traces were described in the material of *G. gaudryi* by Pictet & Humbert. It is possible that Bassani's specimens are close to *G. gaudryi,* but most of the characters which distinguish *Gaudryella* and *Humbertia* are not determinable in them, and nothing is known of the caudal skeleton.

Kramberger (1895 : 37, pl. 8, figs. 3, 4) referred two specimens to *C. gaudryi,* one from Mrzlec (fig. 3) and one from Comen (fig. 4). According to d'Erasmo (1946 : 37) the second of these is *Leptolepis neocomiensis,* the first *Scombroclupea gaudryi,* which in d'Erasmo's usage is a clupeomorph fish. Kramberger did not describe the specimens but only gave a series of measurements and counts taken from the Mrzlec individual. This has a rather large, toothed premaxilla and 38 vertebrae (14 caudal), as in *Humbertia,* but the subopercular is small, the dorsal is set further back than in either *Humbertia* or *Gaudryella* and has only ten rays, while the lower jaw appears to be more slender than it is in *Humbertia* and *Gaudryella.* Once again, nothing is

known of the majority of the features in which *Gaudryella* and *Humbertia* differ, and nothing is known of the caudal skeleton.

Apart from the various European and African Cretaceous *Leptolepis* species referred to *Clupavus* which have been discussed in the previous section, there are several American *Leptolepis*-like species which might be related to *Gaudryella* or *Humbertia*. As in the clupavids, most of these are very poorly known and where nothing can be deduced about their relationships they will merely be listed.

Leptolepis bahiaensis Schaeffer (1947 : 13) and *Scombroclupeoides scutata* Smith Woodward (1908 : 360). These species are from the Neocomian (non-marine lowermost Cretaceous) of Bahia, Brazil. Schaeffer (1947, table 1) placed them in the Upper Cretaceous, but recent work on ostracods (Krömmelbein 1962, Grekoff & Krömmelbein 1967) has shown that the beds correlate with the European and West African Wealden. *Scombroclupeoides scutata* was described by Smith Woodward as a clupeoid, since he found traces of abdominal scutes and thickened scales behind the anal which he compared to the scutes associated with the anal finlets in *Scombroclupea*. But the type material of the species (P.10570–1) shows that the so-called abdominal scute is the front part of the left opercular and subopercular, and the post-anal scutes appear to be lateral line scales. There is thus no evidence that this fish is a clupeoid, but positive evidence of its relationships is lacking since the caudal skeleton is not preserved and the skull is very deficient. Epipleurals are present, suggesting that it is not a *Leptolepis*, but otherwise it is very like Schaeffer's *L. bahiaensis*. The latter is described as having no epipleurals and no caudal scutes, while there is a large caudal scute in *S. scutata*. The Bahia series is correlated with the Cocobeach series of West Africa, and one or both of these Brazilian species could well be close to or synonymous with *Leptolepis congolensis* (p. 286).

Leptolepis tamanensis Dunkle & Maldonado-Koerdell (1953) is from Neocomian beds in Mexico. The only specimen has a *Gaudryella*-like ethmoid region, but is very incomplete.

Leptolepis diasii Santos (1958) is from the Santana Formation of Ceara, Brazil. These marine or estuarine beds were formerly considered to be Upper Cretaceous, but recent workers place them in the Lower Albian or Upper Aptian (Santos & Valenca 1968, Beurlen 1970). The fish has 33–34 vertebrae with ten caudal, many fewer than *Gaudryella* and *Humbertia*.

Leptolepis australis de Saez (1939), *L. leanzai* de Saez (1949), *Tharrhias feruglioi* Bordas (1943) and *T. shamani* de Saez (1949) are all from the continental Upper Cretaceous of Chubut, Argentina. Nothing useful is known of them.

One last Cretaceous fish that must be mentioned is *Idrissia jubae* Arambourg (1955 : 77), from the Lower Cenomanian of Jebel Tselfat, Morocco. Arambourg described this as a primitive member of the Stomiatoidei and placed it in the family Gonostomatidae. Weitzman (1967b: 536) discussed *Idrissia* in his review of fossil stomiatoids and pointed out that there was no reason to regard it as a gonostomatid or even as a stomiatoid relative, principally because of lack of information on its structure. *I. jubae* is superficially very like *Gaudryella* and *Humbertia*, with 40 vertebrae (14 caudals), epineurals and epipleurals on the abdominal vertebrae, a vertical hyomandibular and a small mouth. It differs from *Gaudryella* and *Hum-*

bertia in having a slightly deeper trunk and longer head, the dorsal fin set further back (origin over nineteenth vertebra), a longer anal fin (13 rays), short, slender ribs, and a rather shallow mandible. The premaxilla is toothed and the subopercular is large, as in *Humbertia*, but there are about ten branchiostegals and the pelvics are inserted below the twenty-first vertebra, as in *Gaudryella*.

Apart from the species mentioned in this section and the preceding one, all other Cretaceous teleosts seem to differ markedly from *Gaudryella* and *Humbertia*, and the majority belong to easily recognised groups. One must conclude that although there are various species which resemble *Gaudryella* and *Humbertia*, all are too poorly known for any detailed comparisons and many of these resemblances are simply characters of relatively generalised teleosts. There is no fossil species which can be shown to be more like one of these genera than the other, and therefore no evidence that they are not each other's closest relatives.

V. SUMMARY

1. Two small, superficially *Clupavus*-like or *Argentina*-like fishes are described as *Gaudryella* gen. nov. *gaudryi* (Pictet & Humbert) and *Humbertia operta* gen. & sp. nov. These two monotypic genera are known only in the Middle Cenomanian fish beds of Hakel and Hajula, Lebanon. *Gaudryella gaudryi* is the commonest fish at Hajula but is uncommon at Hakel ; it outnumbers *Humbertia operta* by about three to one at both localities.

2. Because of abundant material which is amenable to acid preparation, the structure of these two species can be worked out in some detail. This excess of knowledge severely limits comparisons with other superficially similar Cretaceous species, none of which is known in comparable detail, and useful comparisons can only be made with living fishes.

3. *G. gaudryi* and *H. operta* share many osteological features (p. 250), apart from overall similarities in body form and fin disposition. The majority of these shared features are primitive teleostean characters, but fusion of the first pre-ural and ural centra, the development of a stegural, passage of the supratemporal commissure in a groove across the parietals, an almost entirely acellular skeleton, and a few other advanced features show that both genera are members of the Euteleostei.

4. There are many differences between *Gaudryella* and *Humbertia* (Table 3), the most striking of which include the form of the ethmoid ossifications (very primitive in *Gaudryella*, *Argentina*-like in *Humbertia*), the distribution of the dentition, the shape and number of the branchiostegals, the presence of a small basipterygoid process and a sutured ceratohyal in *Humbertia*, and fusion between the two posterior infraorbitals, between the pelvic splint and girdle, and within the caudal skeleton in *Gaudryella*. Despite these differences, it is not possible to show that either genus is more closely related to any living or contemporary fish than is the other, or that statements about the relationships of one are not equally true of the other.

5. Amongst euteleostean fishes, there is no evidence in *Gaudryella* or *Humbertia* of the specialisations which characterise the Ostariophysi or the Neoteleostei, and the two genera are placed in the Salmoniformes. Although *Gaudryella* and *Humbertia* resemble the argentinoids in many ways, any close relationship is improbable because

of the cellular skeleton and lack of a stegural in the latter. The only salmoniform groups with which they show positive evidence of relationship are the osmeroids and stomiatoids, especially the hypomesine osmerids, but they are much more primitive than any known member of these suborders and are placed as Salmoniformes *incertae sedis*.

6. The ossifications of the ethmoid region in teleosts are reviewed and it is concluded that a single, peri- and endochondrally ossified mesethmoid and a separate dermal rostral are primitive for teleosts. Paired proethmoids are certainly homologues of the median rostral, but it is not possible to decide which arrangement is the more primitive. The numerous ethmoid ossifications of osmerids and stomiatoids are an advanced feature relating the two groups.

7. The jaws and palate of *Gaudryella* and *Humbertia* are more like those of *Hypomesus* than any other osmeroid or stomiatoid. Evidence is presented that *Hypomesus* is the most primitive osmerid, and that these resemblances may therefore be significant. The large mouths and long, shallow lower jaw of osmerines and the larger mouths of stomiatoids may be successive modifications from a *Hypomesus*-like proto-osmerid.

8. The structure of the caudal skeleton in euteleosteans is reviewed and it is found that they fall into two groups according to whether the neural arch of PU1 (and U1 where this exists) fuses with the underlying centrum, or with the first uroneural to produce a stegural (Fig. 47). The first of these groups, without a stegural, contains the alepocephaloids, argentinoids, galaxioids and ostariophysans ; the second, with a stegural, the salmonoids, esocoids, *Gaudryella* and *Humbertia*, osmeroids, stomiatoids and neoteleosts. The development of the neural spine of PU2 correlates with such a division. The structure of the caudal skeleton indicates that the Prototroctidae and Retropinnidae are osmeroids, not galaxioids.

9. In general, the caudal skeleton seems to be a more reliable guide to relationships (at the level under discussion in this paper) than any known feature or combination of features in the skull, vertebral column or fins. This may well be only because the caudal skeleton is relatively simple and easy to interpret in comparison with the skull, where the significance and the interaction of many features are still poorly understood. But the reliability of the caudal skeleton can be of great value to palaeontologists, for the details of the tail can often be made out in otherwise unpromising fossils.

10. Species placed in the late Jurassic and Cretaceous family Clupavidae are reviewed, and it is concluded that they show no evidence of close relationship. Most of these species are so poorly known that nothing can be said about their relationships. The type-species of *Clupavus*, *C. maroccanus*, is apparently a euteleostean, not a clupeomorph, but it is not close to *Gaudryella* and *Humbertia*.

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VII. ABBREVIATIONS USED IN FIGURES

acv	foramen of anterior cerebral vein
Ao	antorbital
arpm	articular process of premaxilla
Art	angulo-articular
Asp	autosphenotic
aspm	ascending process of premaxilla
Bh	basihyal
Bht	basihyal tooth plate
Boc	basioccipital
bpt	basipterygoid process
Brr	branchiostegal ray
Cl	cleithrum
Cor	coracoid
csc	caudal scute
Dch	distal ceratohyal
Den	dentary
Dsp	dermosphenotic
Ecp	ectopterygoid
Enp	endopterygoid
ep	epural
Epo	epiotic
epsa	foramen or groove for efferent pseudobranchial artery
Exo	exoccipital
fh	hypural foramen (between first and second hypurals)
fhm	articular surface for hyomandibular
fica	foramen of internal carotid artery
fotn	foramen of otic branch of facial nerve
fph	parhypural foramen (between parhypural and first hypural)
Fr	frontal
h1-6	hypurals
hap	hypurapophysis
Hhl	lower hypohyal
Hhu	upper hypohyal
Hm	hyomandibular
hmx	cranial condyle of maxilla
Ic	intercalar
Io2-5	infraorbitals
Iop	interopercular
Lac	lachrymal
Le	lateral ethmoid
Mes	mesethmoid
Mpt	metapterygoid
Mx	maxilla
myo	posterior opening of myodome
Na	nasal
npu1	neural arch of first pre-ural centrum
npu2	neural spine of second pre-ural centrum
nu1	neural arch of first ural centrum
Op	opercular
Ors	orbitosphenoid
Pa	parietal
Pal	palatine
Pas	parasphenoid
Pch	proximal ceratohyal
pfmx	palatine condyle on maxilla
ph	parhypural
Pmx	premaxilla
Pop	preopercular
Pro	prootic
ptf	opening of post-temporal fossa
ptfc	posterior opening of trigemino-facialis chamber
Pto	pterotic
Pts	pterosphenoid
Ptt	post-temporal
pu1 + u1	compound centrum containing first pre-ural and ural centra
pu3-4	third and fourth pre-ural centra
Qu	quadrate
Ro	rostral
Rrt	retroarticular
Sca	scapula
Scl	supracleithrum
scr	ossified sclerotic
Sma	anterior supramaxilla
Smp	posterior supramaxilla
So	supraorbital
Soc	supraoccipital
son	foramina of superficial ophthalmic nerves
Sop	subopercular
st	stegural
Stt	supratemporal
stv	foramen of supratemporal branch of vagus nerve
Sym	symplectic
u2	second ural centrum
ud	urodermal
Uh	urohyal
un1-3	uroneurals
Vo	vomer
IV, VIIhm, IX, X	foramina of trochlear, hyomandibular trunk of facial, glossopharyngeal and vagus nerves

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PLATE 1

Fig. 1. ***Gaudryella gaudryi*** (Pictet & Humbert), P.48047, a transfer preparation.
Fig. 2. Positive print of a radiograph of the specimen in Fig. 1.
Fig. 3. ***Humbertia operta*** gen. & sp. nov., AM 3808.
All × 2.2. Specimens from the Middle Cenomanian, Hajula, Lebanon, showing preservation in lateral view, which is unusual.

1

2

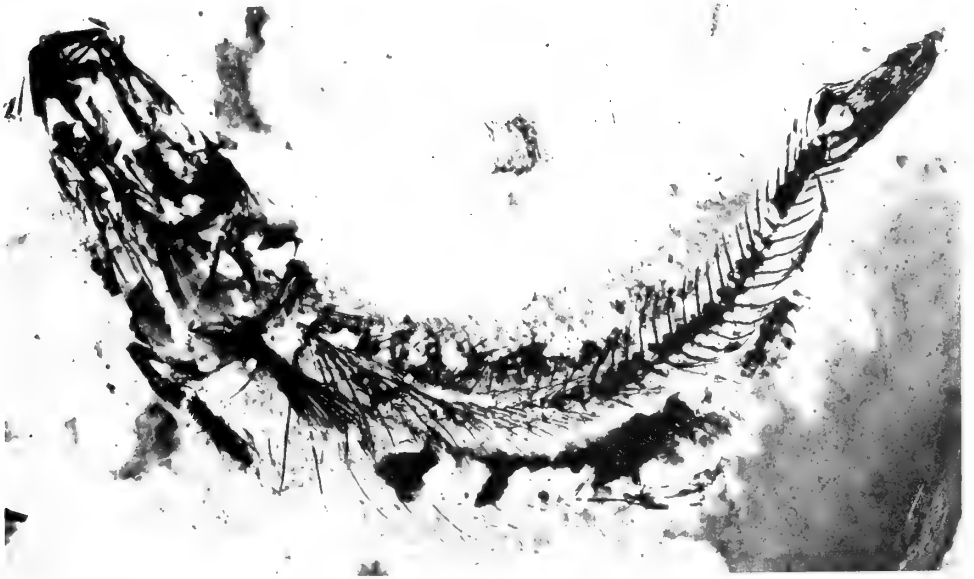
3

PLATE 2

Fig. 1. ***Gaudryella gaudryi*** (Pictet & Humbert), P.9991.

Fig. 2. ***Humbertia operta*** gen. & sp. nov., AM 4590.

Both × 2.4. Transfer preparations from the Middle Cenomanian, Hajula, Lebanon, showing typical curvature of the trunk and oblique crushing of the skull.



1

2

PLATE 3

Fig. 1. ***Humbertia operta*** gen. & sp. nov., P.48218 (holotype), Middle Cenomanian, Hakel, Lebanon, × 1·7.

Fig. 2. ***Gaudryella gaudryi*** (Pictet & Humbert), P.48060, Middle Cenomanian, Hajula, Lebanon, × 2·9.

Both specimens unprepared, showing typical curvature of the trunk.

1

2

PLATE 4

Fig. 1. ***Gaudryella gaudryi*** (Pictet & Humbert), AM 3783, × 3.
Fig. 2. ***Humbertia operta*** gen. & sp. nov., P.51260, × 3·7.
Both from the Middle Cenomanian, Hajula, Lebanon, positive prints from radiographs of transfer preparations.

2

PLATE 5

FIG. 1. AM 4115, a skull of *Humbertia operta* gen. & sp. nov. crushed dorso-ventrally and showing the gill skeleton (cf. Fig. 25) and (top left) a skull of *Gaudryella gaudryi* (Pictet & Humbert), × 3.1.

FIG. 2. *Humbertia operta* gen. & sp. nov., AM 4411, × 3.2.

Both from the Middle Cenomanian, Hajula, Lebanon, positive prints from radiographs of transfer preparations.

1

2

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SCOTTISH CALLOVIAN AND OXFORDIAN OSTRACODA

R. C. WHATLEY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY VOL. 19 No. 6
LONDON: 1970

SCOTTISH CALLOVIAN AND OXFORDIAN OSTRACODA

BY

ROBIN CHARLES WHATLEY

Pp. 297–358 ; 15 *Plates*, 9 *Text-figures*

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SCOTTISH CALLOVIAN AND OXFORDIAN OSTRACODA

By R. C. WHATLEY

CONTENTS

		Page
I.	Introduction and acknowledgements	301
II.	Location and stratigraphy	304
III.	Systematic descriptions	311
	Subclass Ostracoda Latreille	311
	Order Myodocopida Sars	311
	Suborder Cladocopina Sars	311
	Family Polycopidae Sars	311
	Genus *POLYCOPE* Sars	311
	Polycope pelta Fischer	311
	Polycope sububiquita n. sp.	312
	Order Podocopida Müller	313
	Suborder Platycopina Sars	313
	Family Cytherellidae Sars	313
	Genus *CYTHERELLA* Jones	313
	Cytherella fullonica (Jones & Sherborn)	313
	Suborder Podocopina	314
	Superfamily Bairdiacea Sars	314
	Family Macrocypridae Müller	314
	Genus *MACROCYPRIS* Brady	314
	Macrocypris aequabilis Oertli	314
	Superfamily Cypridacea Baird	314
	Family Paracyprididae Sars	314
	Genus *PARACYPRIS* Sars	314
	Paracypris sp. A.	314
	Family Pontocyprididae Müller	315
	Genus *ARGILLOECIA* Sars	315
	Argilloecia (?) sp. A.	315
	Family Krausellidae Berdan	316
	Genus *KRAUSELLA* Ulrich	316
	Krausella sp. A.	316
	Superfamily Cytheracea Baird	316
	Family Schuleridеidae Mandelstam	316
	Subfamily Schuleridеinae Mandelstam	316
	Genus *PRAESCHULERIDEA* Bate	316
	Praeschuleridea batei n. sp.	316
	Family Bythocytheridae Sars	318
	Genus *MONOCERATINA* Roth	318
	Monoceratina scrobiculata Triebel & Bartenstein	318
	Monoceratina stimulea (Schwager)	319
	Monoceratina vulsa (Jones & Sherborn)	319
	Monoceratina sp. A.	320

Family CYTHERIDEIDAE Sars 320
Subfamily CYTHERIDEINAE Sars 320
Genus *GALLIAECYTHERIDEA* Oertli . . 320
Galliaecytheridea staffinensis n. sp. . . 320
Genus *GLABELLACYTHERE* Wienholz . . 321
Glabellacythere reticulata n. sp. . . . 321
Glabellacythere dolabra (Jones & Sherborn) 323
Family CYTHERURIDAE Müller 323
Genus *PROCYTHERURA* n. gen. . . . 323
Procytherura tenuicostata n. sp. . . 324
Genus *EUCYTHERURA* Müller . . . 324
Subgenus *VESTICYTHERURA* Gründel
Eucytherura (*Vesticytherura*) *costaeiregularis* n. sp. 325
Eucytherura (*Vesticytherura*) *horrida* n. sp. 327
Eucytherura (*Vesticytherura*) *scottia* n. sp. 328
Genus *CYTHEROPTERON* Sars . . . 329
Cytheropteron aquitanum Donze . . 329
Genus *METACYTHEROPTERON* Oertli . 329
Metacytheropteron sutherlandensis n. sp. 329
Metacytheropteron sp. A. . . . 330
Genus *PEDICYTHERE* Eagar . . . 331
Pedicythere anterodentina n. sp. . . 331
Family PROGONOCYTHERIDAE Sylvester-Bradley . 332
Subfamily PROGONOCYTHERINAE Sylvester-Bradley 332
Genus CAYTONIDEA Bate 332
Caytonidea terraefullonicae (Jones & Sherborn) 332
Genus *LOPHOCYTHERE* Sylvester-Bradley . 332
Subgenus *LOPHOCYTHERE* Sylvester-Bradley 333
Lophocythere (*Lophocythere*) *scabra bucki* Lutze 334
Lophocythere (*Lophocythere*) *interrupta interrupta* Triebel . . . 335
Subgenus *NEUROCYTHERE* n. subgen. . 336
Lophocythere (*Neurocythere*) *cruciata alata* n. subsp. 336
Lophocythere (*Neurocythere*) *cruciata intermedia* Lutze . . . 338
Lophocythere (*Neurocythere*) *cruciata oxfordiana* Lutze . . . 339
Lophocythere (*Neurocythere*) *cruciata cruciata* Triebel 340
Lophocythere (*Neurocythere*) *flexicosta lutzei* n. subsp. 341
Genus *FUHRBERGIELLA* Brand & Malz . 343
Subgenus *PRAEFUHRBERGIELLA* Brand & Malz 343
Fuhrbergiella (*Praefuhrbergiella*) *horrida horrida* Brand & Malz . 343
Family PROTOCYTHERIDAE Lyubimova . . . 343

Subfamily PLEUROCYTHERINAE Mandelstam . . 344
Genus *PALAEOCYTHERIDEA* Mandelstam . 344
Palaeocytheridea parabakirovi Malz . 344
Genus *PLEUROCYTHERE* Triebel . . 344
Pleurocythere borealis borealis n. subsp. . 345
Pleurocythere borealis carinata n. subsp. . 346
Pleurocythere caledonia n. sp. . . . 348
Subfamily KIRTONELLINAE Bate 349
Genus *PSEUDOHUTSONIA* Wienholz . . 349
Pseudohutsonia hebridica n. sp. . . 349
Pseudohutsonia sp. A. 351
Genus *PSEUDOPERISSOCYTHERIDEA* Mandelstam 351
Pseudoperissocytheridea parahieroglypica n. sp. 352
IV. REFERENCES 353
V. APPENDIX 356
ADDENDUM 358

SYNOPSIS

Thirty-eight species of Ostracoda, of which 16 species and subspecies are new, are described from Callovian and Oxfordian strata at three areas of outcrop in Scotland. These species belong to 23 genera of which one *PROCYTHERURA* and one subgenus *LOPHOCYTHERE* (*NEUROCYTHERE*) are new. The stratigraphy of the three areas is briefly described.

I. INTRODUCTION AND ACKNOWLEDGEMENTS

THE present work is the first of a series of papers concerning the Ostracoda of the Callovian and Oxfordian stages of Great Britain. The ostracod faunas of these two stages have, in Britain, been almost entirely neglected and the only published information, with the exception of one short paper by the author (Whatley 1964) has been contributed by foreign workers. Malz in two papers in 1958, and Lutze in 1960 have described faunas from southern England and Glashoff (1964) has made a regional survey of the Oxfordian fauna of England and Scotland. The substantial number of new taxa described in the present series of papers is evidence of the largely incidental nature of the preceeding studies.

Although this first paper is principally concerned with the Callovian and Oxfordian faunas of Scotland, in the case of certain species, material from England has been utilized to facilitate a more complete description.

In the description of the Ostracoda, the following convention is employed :

	mm.
Very small	<0·4
Small	0·4–0·5
Medium	0·5–0·7
Large	0·7–0·9
Very large	>0·9

This work was undertaken in the Department of Geology, University of Hull, during the tenure of a DSIR/SRC Studentship. The author is considerably indebted to Professor D. T. Donovan (late of that Department), to Dr. J. W. Neale

TABLE 1

SYSTEM	STAGE		ZONE	MAJOR STRATIGRAPHICAL UNITS	STAFFIN BAY	BRORA	PORT-AN-RIGH
	OXFORDIAN	UPPER	pseudocordata	UPPER CALCAREOUS GRIT	Staffin Shales	not known	not known
			cautisnigrae	GLOS OOLITE SERIES			
			plicatilis	OSMINGTON OOLITE SERIES BERKSHIRE OOLITE SERIES			Port-an-Righ Sandstone: sandstones and sandy shales
		LOWER	cordatum	LOWER CALCAREOUS GRIT		sandstones, limestones and sandy shales Brora sandstone / white sandstone	Port-an-Righ Ironstone: sandstones and ironstones
			mariae	OXFORD CLAY	Shales with thin cementstones	Clynelish Quarry Sandstone / white, fine-grained silicified sandstone	shales
	CALLOVIAN		lamberti			Fascally Sandstone / ferruginous sandstone	
			athleta			Fascally Shale / sandy shales	not known
			coronatum		Shales with thin limestone at base	Brora Brick Clays / grey and blue clays	
			jason		black micaceous shale	Brora Shales / green and khaki shales	shales
			calloviense	KELLAWAYS ROCK	not known	? absent	? absent
			koenigi	KELLAWAYS CLAY		Brora Roof Bed hard calcareous sandstone	
			macrocephalus	UPPER CORNBRASH	Red nodular limestone	Possibly developed as part of Great Estuarine Series	not known

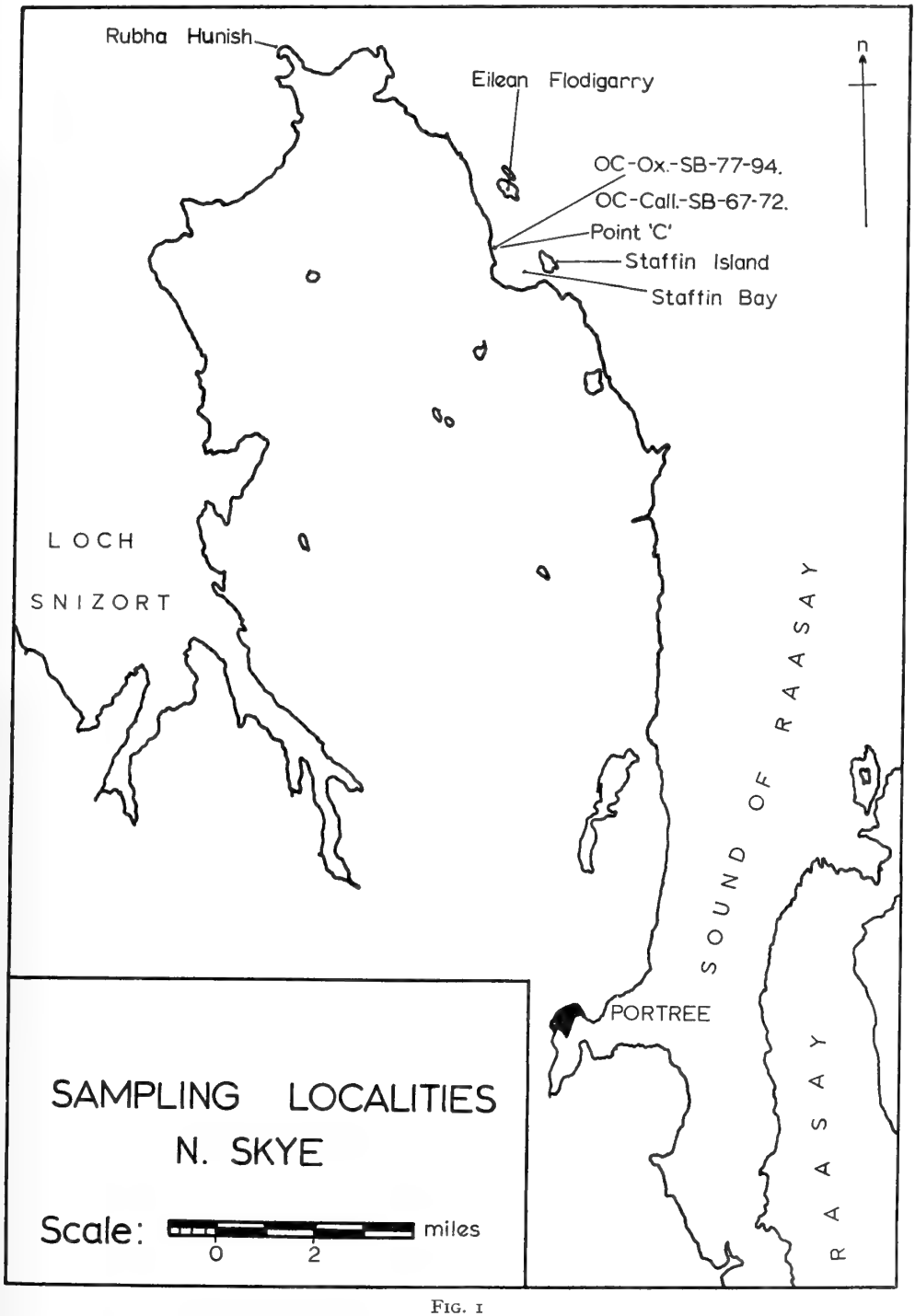
Rubha Hunish
Eilean Flodigarry
N
OC-Ox.-SB-77-94.
OC-Call.-SB-67-72.
Point 'C'
Staffin Island
Staffin Bay
LOCH
SNIZORT
SOUND OF RAASAY
PORTREE
RAASAY
SAMPLING LOCALITIES
N. SKYE
Scale:
miles
0
2

FIG. 1

and Mr. L. F. Penny for their encouragement and assistance during the completion of this work. My thanks are also due to members of the technical staff at Hull, in particular to Mr. N. Bell, for valuable assistance. Additionally, permission to deposit type specimens in the British Museum (Natural History), granted by the University of Hull on the recommendation of Professor M. R. House and Dr. J. W. Neale is gratefully acknowledged.

The author has received very considerable assistance from colleagues in this country and abroad and gratefully acknowledges receipt of copies of their work and of specimens for comparison. In particular my thanks are due to Dr. R. H. Bate of the British Museum (Natural History) for a great deal of assistance and encouragement.

Lastly my grateful thanks are due to Professor Alan Wood for his support in preparing this paper ; to my friend and colleague, Dr. J. R. Haynes, for critically reading the manuscript and to Mr. H. Williams for technical assistance. Mr. P. Sherrington kindly drew Fig. 6, and Miss P. Matthews and Miss G. Jones typed the manuscript.

The ostracods described in this paper have been deposited in the collections of the University of Hull (prefix HU.) and in the British Museum (Natural History) (prefix Io.)

II. LOCATION AND STRATIGRAPHY

Deposits of Jurassic age occur on a number of Inner Hebridean Islands and the adjacent mainland and also along the north-east coast of Scotland in Ross and Sutherland. Callovian and Oxfordian strata occur in both of these areas although their outcrops are somewhat restricted.

Samples have been collected from three localities :

1. From the Callovian and Oxfordian of Staffin Bay, Trotternish, Skye.
2. From the Callovian of Brora, Sutherland.
3. From the Oxfordian of the Ross Peninsular at Port-an-Righ.

A summary of the Callovian and Oxfordian Strata in these areas is given in Table 1.

1. *Staffin Bay.* (Fig. 1.)

The succession at Staffin Bay consists largely of a thick sequence of blue and grey marine shales with a few thin cementstones. These beds were first described by Macculloch (1819, p. 345) and were later shown by Forbes (1851) to be equivalent to the Oxford Clay of England. Macgregor (1934, p. 397) has described the section in detail and it is from his locality at point ' C ' (NG473694) that the present samples were collected. Using the evidence of the abundant ammonite fauna in the succession, Macgregor identified strata of Lower and partly Upper Oxfordian age. Anderson, (1961, p. 23) mentions an early record of ammonites indicating the presence of zones from the *jason* to the *cordatum* followed by Upper Oxfordian strata of the same facies. Cordey (1962) working on foraminifera from the section at point 'C' demonstrated the presence of the *lamberti*, *mariae* and *cordatum* zones, this evidence being augmented by the identification of ammonites collected by Cordey from this section by Dr. J. H. Callomon.

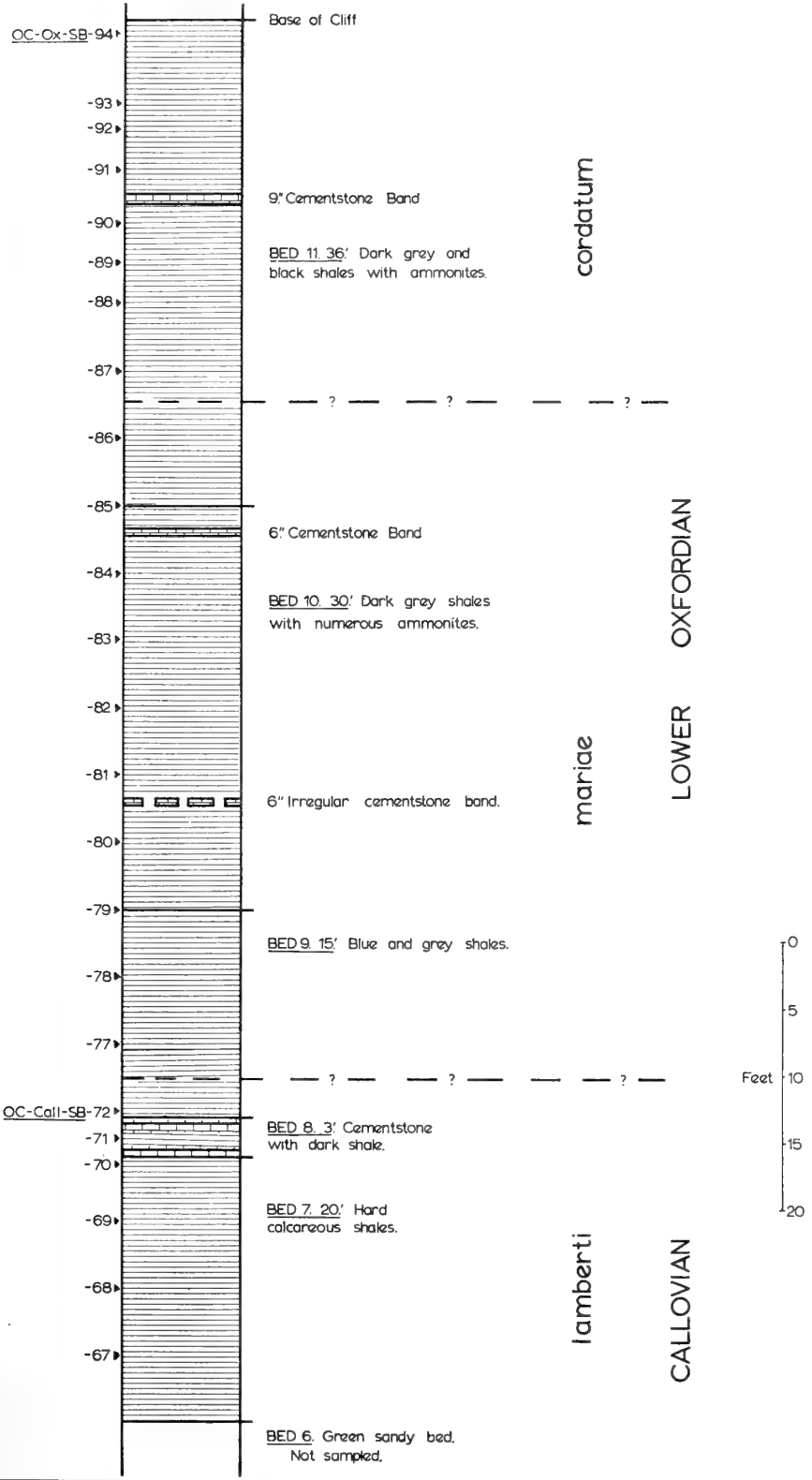

FIG. 2. The stratigraphical succession and the position of the samples at Staffin Bay.

The most recent works on the Staffin Bay succession are by Turner and Anderson, both in 1966. Both workers give detailed accounts of the succession which, however, differ somewhat in thickness of various units and in the position of the zonal boundaries. Both workers do, however, recognize strata with ammonites below the *lamberti* zone. The evidence from the Ostracoda is such that the *lamberti*, *mariae* and *cordatum* zones can be recognized and compared to similar strata elsewhere in Britain. The section measured and collected by the author is given in Fig. 2.

Unfortunately, the two lowest samples were barren of either ostracoda or foraminifera and the age of these lowest shales, which may belong to the *athleta* zone cannot be resolved.

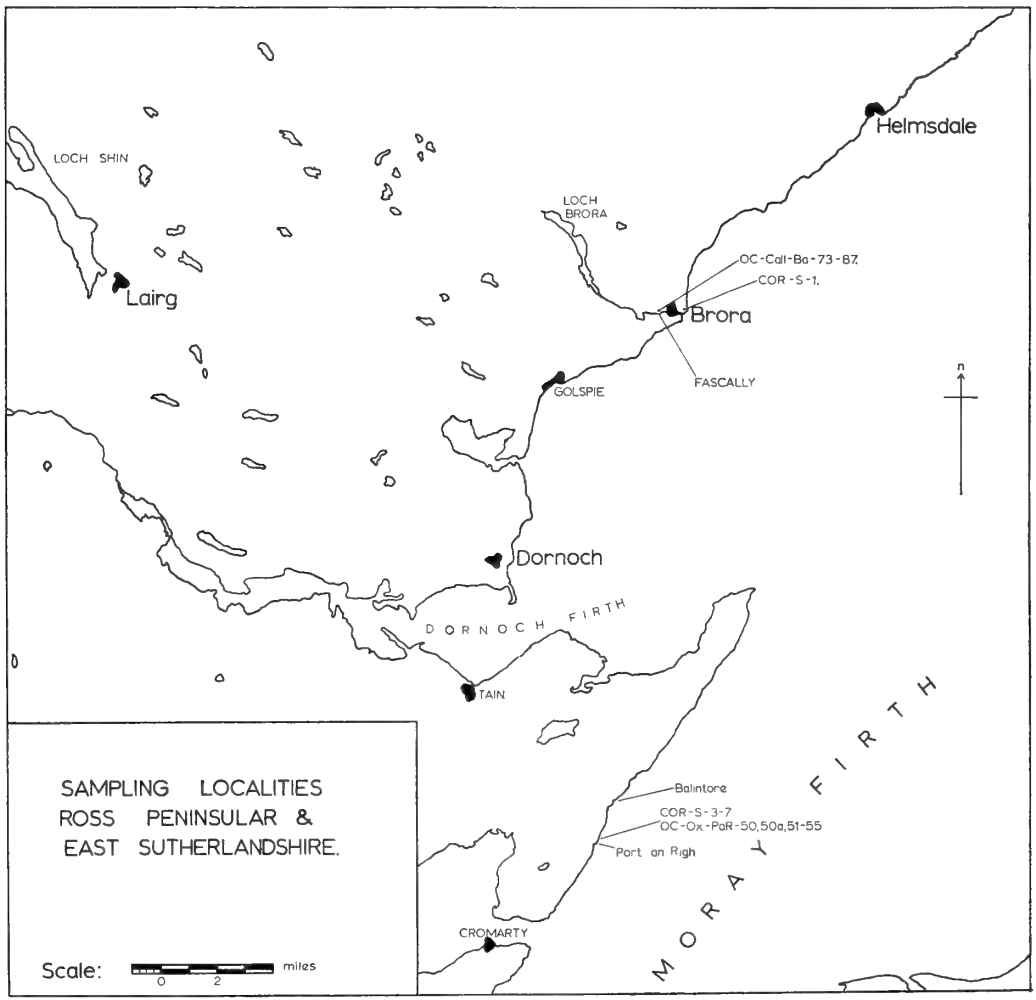

FIG. 3

SAMPLES

OC-Call-Ex

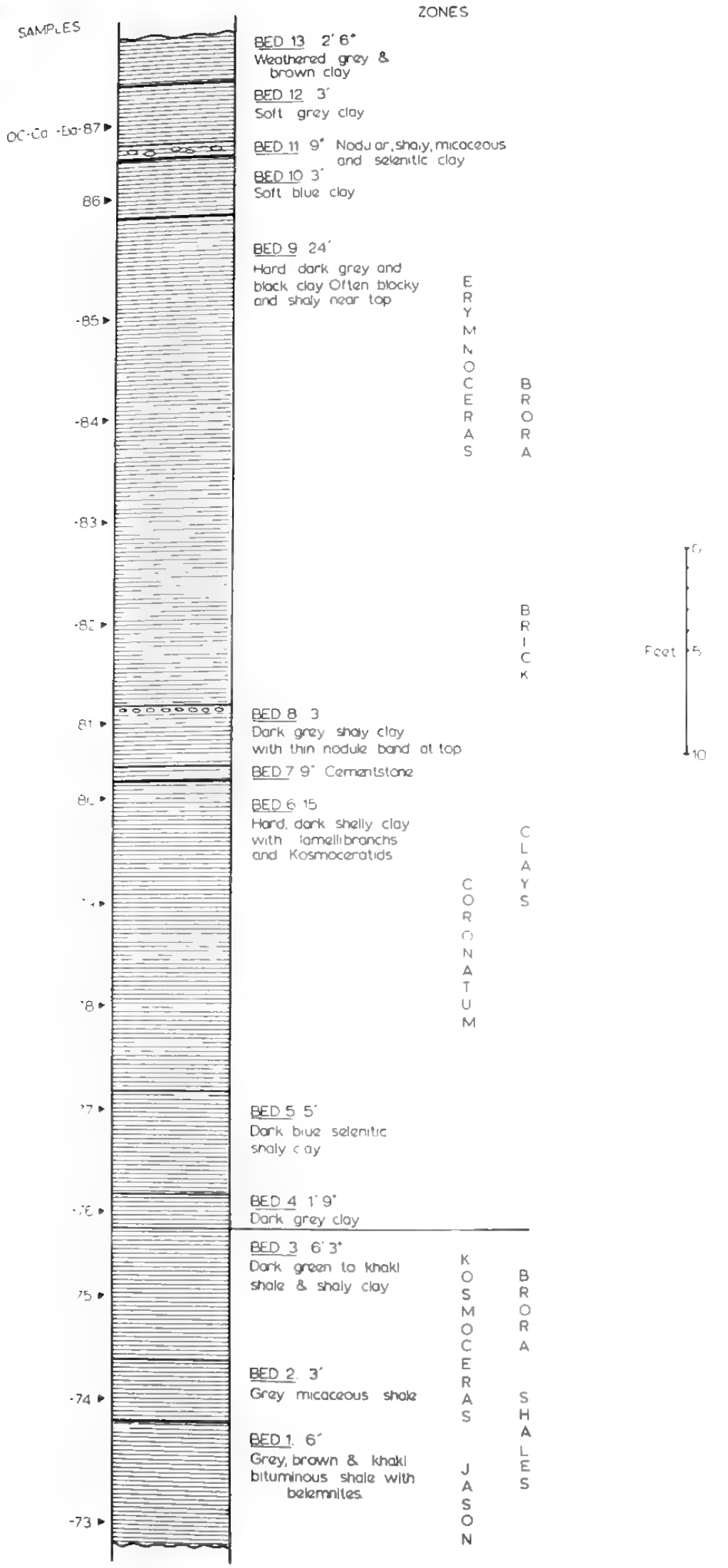

FIG 4 The stratigraphical succession and position of samples at Fascally brick pit, Brora.

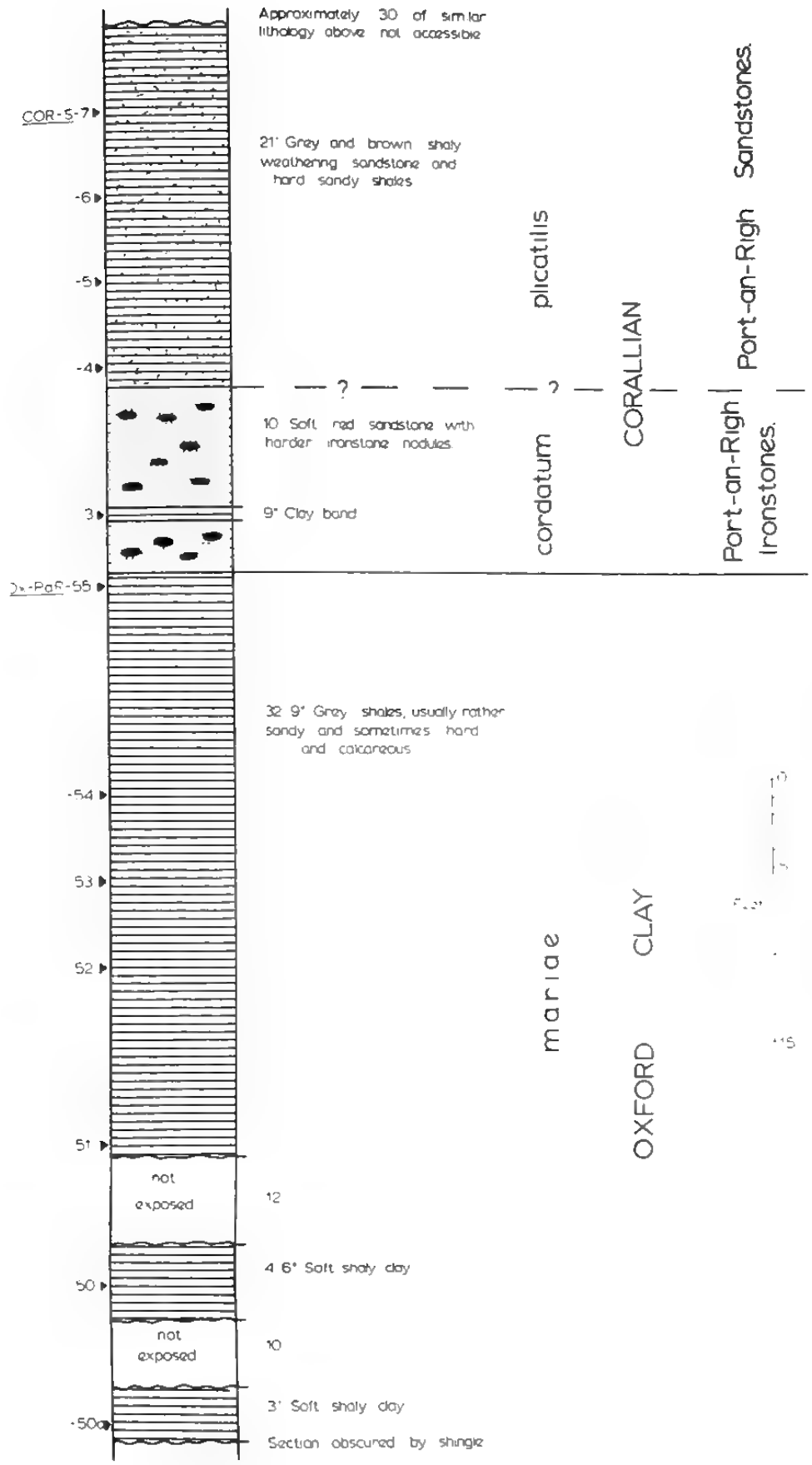

FIG 5 The stratigraphical succession and position of samples at Port-an-Righ.

The overlying Upper Oxfordian shales were badly exposed in 1963 and only a few poorly located samples were collected. Unfortunately, both these and those kindly sent to the author by Judith Turner, proved to be barren of ostracods.

2. *Brora.* (Fig. 3.)

Callovian and Oxfordian strata occur amongst the narrow strip of Jurassic deposits along the east coast of Sutherlandshire, between Golspie and Helmsdale. They are best displayed around Brora and are often of different facies to their equivalents in England and elsewhere in Scotland. The *macrocephalus* zone is not recognized but may be present as a non-marine facies of the Great Estuarine Series. The first deposit with undisputed Callovian fossils is the Brora Roof Bed which contains ammonites

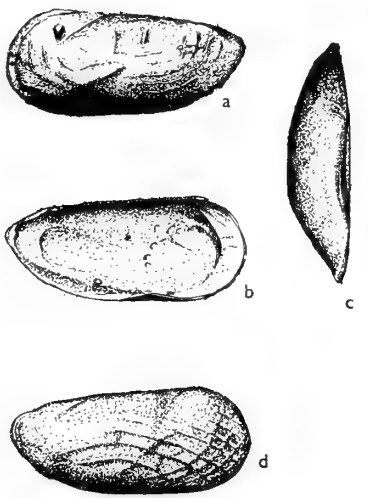

FIG. 6. *Procytherura tenuicostata* Gen. et. sp. n. A-C, Left valve, holotype (HU.18.J.30). a. External view ; b. internal view ; c. dorsal view. d. Right valve, paratype (HU.18.J.31). External view.

indicative of the *koenigi* zone. The succeeding Brora Shales and Brora Brick Clays are probably of *jason* and *coronatum* zone age respectively although the ammonites have not yet been worked out in detail. Although Ostracoda are abundant in the Brora Brick Clays, in the succeeding Callovian and Oxfordian deposits, which are to a large extent arenaceous in character, some twenty samples failed to reveal a single specimen and are not recorded here. A summary of the Callovian and Oxfordian succession at Brora is given in Table 1. and the details of the succession in the *jason* and *coronatum* zones, at the Fascally coal mine brick pit (NC 898042), together with the position of the samples, is given in Fig. 4.

3. *Port-an-Righ.* (Fig. 3).

Middle and Upper Jurassic strata are exposed on the Ross Peninsular some 30 miles south of Brora. Here, at Port-an-Righ (NH 854734), a series of small intertidal

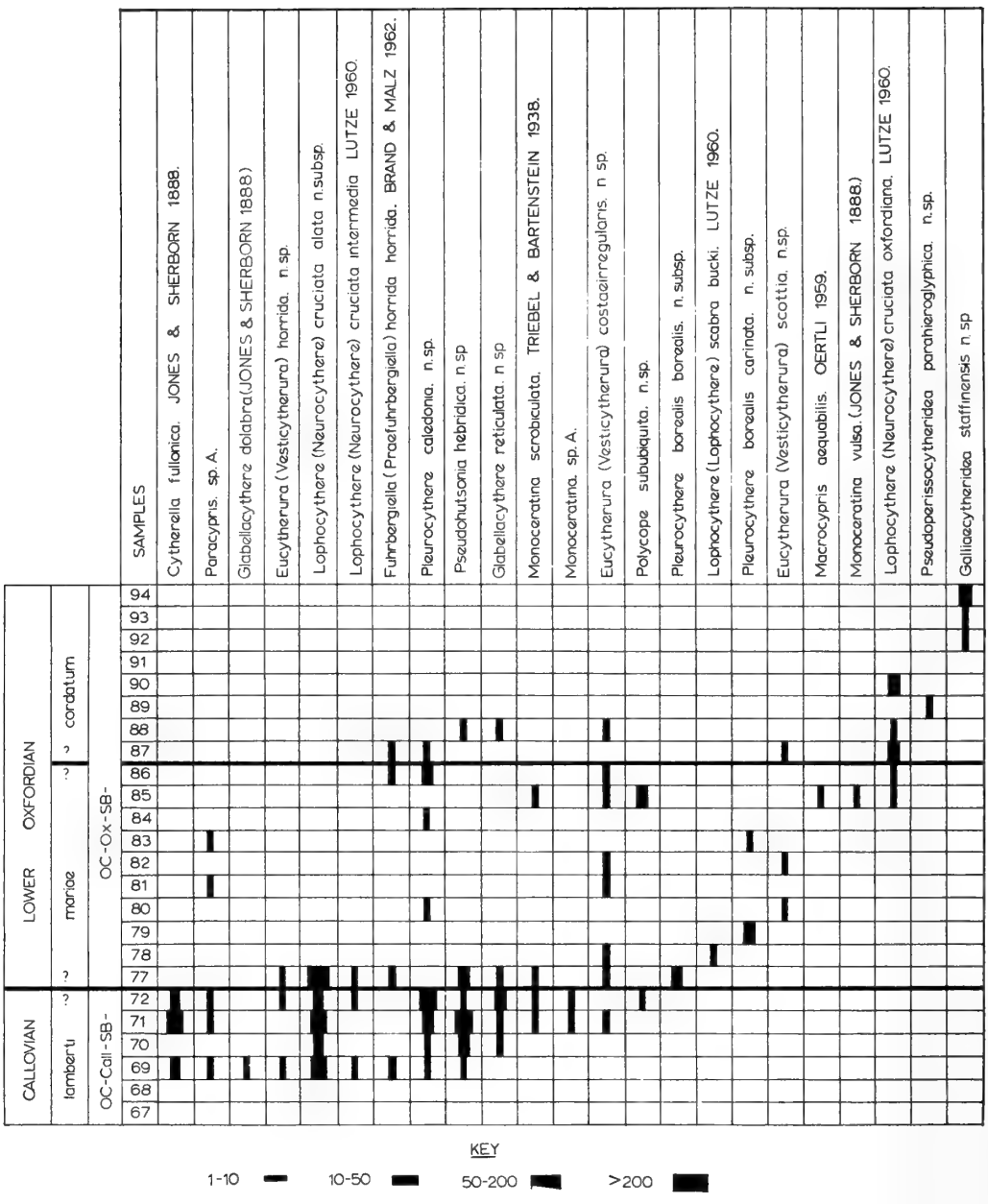

FIG. 7. Distribution of the ostracoda in the Staffin Bay Succession.

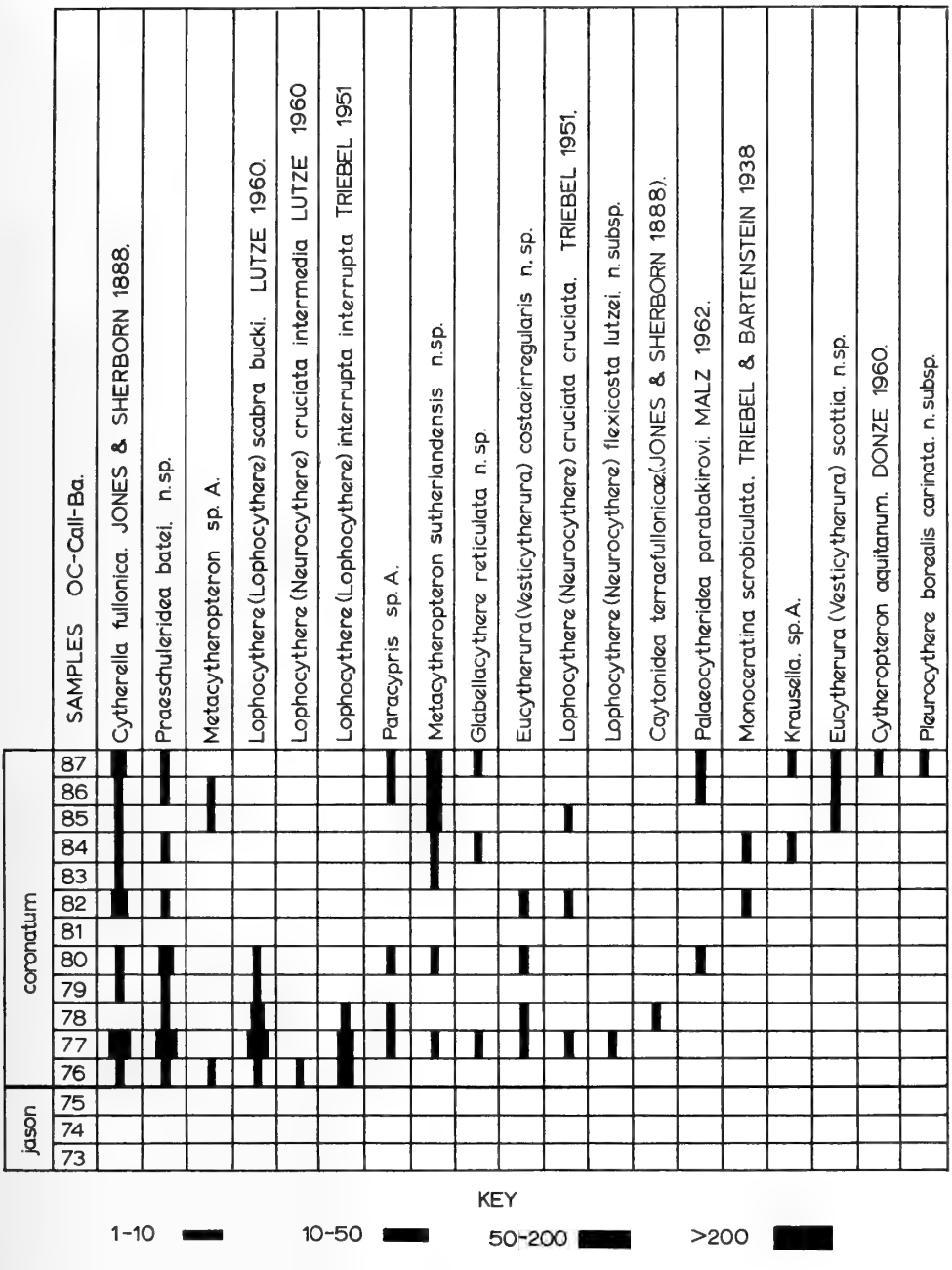

FIG. 8. The distribution of the ostracoda at Fascally Brick Pit, Brora.

outcrops have been preserved by downfaulting against Old Red Sandstone and Moines along a large fault line which may be connected to the Great Glen Fault.

The succession begins with the Brora Roof Bed, and, as at Brora, the succeeding *calloviense* zone seems to be absent. When collected by the author in 1963, the lowest clays and shales of the Callovian were obscured and the lowest beds seen were shales of the *mariae* zone. These are succeeded by the Port-an-Righ Ironstone and Sandstone of *cordatum* and *plicatilis* zone age respectively. The general succession in this area is shown in Table 1 and the section measured and collected by the author in Fig. 5.

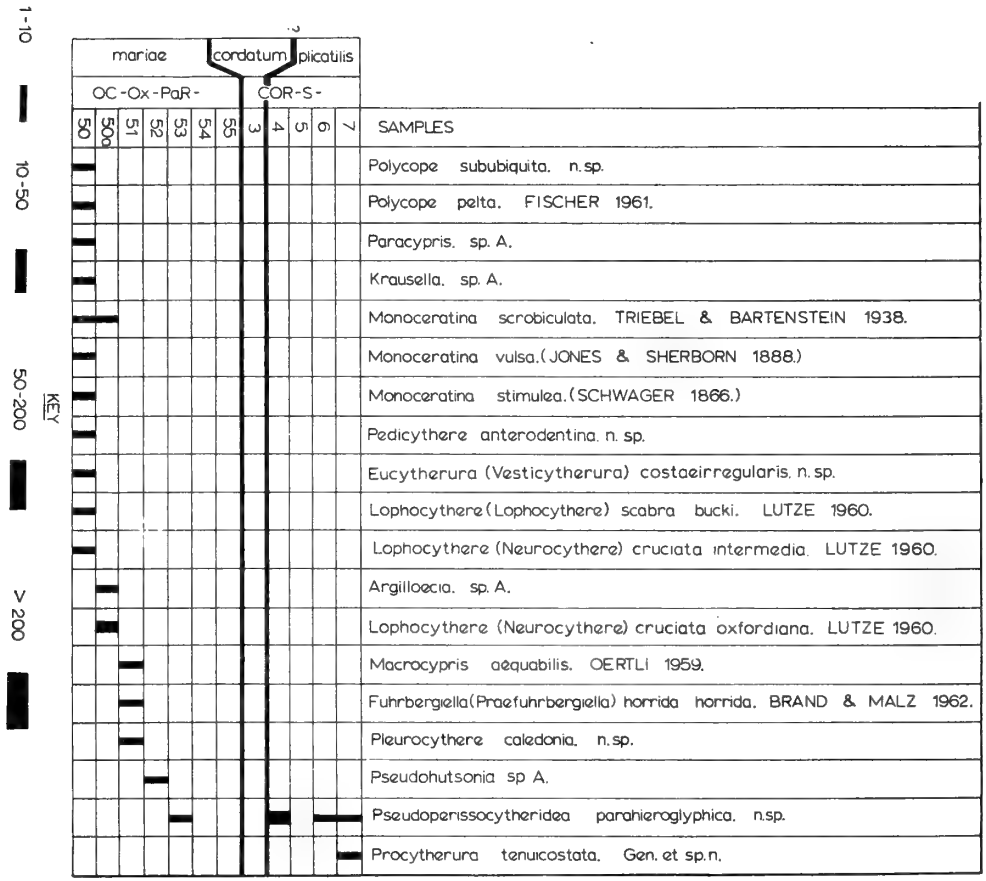

FIG. 9. The distribution of the ostracoda at Port-an-Righ.

The vertical distribution of the Ostracoda at Staffin Bay, Brora and Port-an-Righ is given in Figs. 7, 8 and 9 respectively.

It is not intended to discuss the stratigraphical and palaeoecological potential of these faunas at this stage. However, when the author's taxonomic work on the

Callovian and Oxfordian Ostracoda of England has been published, it is intended that this will be followed by a detailed appraisal of the Stratigraphic, phylogenetic and palaeoecological implications of the Ostracoda from British strata of these two stages as a whole.

The samples used in this study are notated in the following manner :

OC	=	Oxford Clay
Call	=	Callovian
COR	=	Corallian
Ox	=	Oxfordian

1. Staffin Bay
   OC–Call–SB–67 to 72
   OC–Ox–SB–77 to 94
   Stratigraphical position as shown in Fig. 2.
2. Brora
   OC–Call–Ba–73 to 87
   Stratigraphical position as shown in Fig. 4.
3. Port-an-Righ
   OC–Ox–PaR 50 to 55
   COR–S–3 to 7
   Stratigraphical position as shown in Fig. 5.

III. SYSTEMATIC DESCRIPTIONS

Subclass *OSTRACODA* Latreille 1806

Order MYDOCOPIDA Sars 1866

Suborder CLADOCOPINA Sars 1866

Family **POLYCOPIDAE** Sars 1866

Genus ***POLYCOPE*** Sars 1866

Polycope pelta Fischer 1961

Plate 1. Figs. 1–4.

1938 Ostracode 227 Wicher : pl. 27, fig. 4.
1956 *Polycope* sp. 227 (Wicher 1938) Apostolescu and Bourdon: table 2.
1961 *Polycope pelta* n. sp. Fischer, 1961 b: 499, pl. 2 mitte.
1962 *Polycope* sp. B. Donze : 127, pl. 1, fig. 2.
1963 *Polycope pelta* Fischer 1961. Plumhoff : 17 and 18, pl. 1, figs. 1, 2.

MATERIAL. One complete carapace, (Io.5030), from the *mariae* zone of Port-an-Righ.

DIMENSIONS. The dimensions of a second specimen from the *athleta* zone of Oxfordshire are as follows. Length 0·41 ; height 0·41 ; width 0·23.

REMARKS. This species has not previously been recorded from above the Aalenian and this is the first record from Britain.

Polycope sububiquita n. sp.

Plate 1. Figs. 5–11, 15.

1958 *Polycope* sp. 11. Bizon: 21.
1959 *Polycope* sp. 11. Oertli: 15, pl. 1, fig. 1.
1962 *Polycope* sp. A. Donze: 127, pl. 1, fig. 1.
1964 *Polycope* sp. 11. Glashoff : 53, 54, pl. 5, fig. 22.
1964 *Polycope* sp. 12. Glashoff : 54, pl. 5, fig. 21.

DIAGNOSIS. *Polycope* with outline varying from subovate to subcircular, and angle of anterior margin above mid-height. Dorsal margin of variable length, straight or slightly convex. Smooth or with weak reticulations.

HOLOTYPE. One carapace, HU.16.J.5. From the *mariae* zone of Woodham brickpit Oxfordshire. Sample OC–Ox–Wm–5.

MATERIAL. 256 specimens, mostly carapaces.

DISTRIBUTION. Ranging from the *athleta* to the *mariae* zone in England, and occurring in the *mariae* zone at Port-an-Righ, and in the *lamberti* and *mariae* zones of Staffin Bay.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
Carapace	HU.16.J.5	0·43	0·35	0·23
PARATYPES from sample OC–Call–Wm–24. *-athleta* zone Woodham.				
Carapace	Io.5031	0·37	0·35	0·23
Carapace	Io.5032	0·41	0·35	0·23
Carapace	Io.5033	0·39	0·33	0·23
Carapace	Io.5034	0·40	0·33	0·24

DESCRIPTION. Small to very small. Subovate to sublenticular. Valves subequal. Anterior margin with angle at or above mid-height. Posterior margin with well-rounded and obtuse cardinal angle.Ventral margin convex ; dorsal margin variable, usually short, straight or slightly convex. Maximum dimensions : height; just posterior to the anterior cardinal angle, length; at mid-height, width; dorso-medianly.

Ornament smooth or reticulate. Marginal areas very narrow ; inner margin and line of concrescence apparently diverging throughout.

ONTOGENY. The penultimate and preceeding growth stages occur and have the following dimensions. (*athleta* zone, Woodham) :

	Length	Height
Penultimate instar (carapace)	0·32	0·27
Ante-penultimate instar (carapace)	0·25	0·24

REMARKS. The instars are more symmetrically lenticular than the adults. This is an extremely variable species as regards both shape (subovate to sublenticular) and ornament (smooth to reticulate). The range on the continent would seem to be from the Callovian to the Kimmeridgian. Glashoff differentiates two species, 11 and 12 the former being more circular than the latter. In the present material, there is a

complete range of variation between the two types which are consequently considered to be conspecific.

Order PODCOPIDA Müller 1894

Suborder PLATYCOPINA Sars 1866

Family **CYTHERELLIDAE** Sars 1866

Genus ***CYTHERELLA*** Jones 1849

Cytherella fullonica Jones & Sherborn 1888

Plate 1. Figs. 12–14, 16, 18.

1888 *Cytherella fullonica* n. sp. Jones & Sherborn : 274, pl. 1, figs. 12a-c.
1963 *Cytherella fullonica* Jones & Sherborn 1888. Bate : 184, pl. 1, figs. 1, 2.
1963 *Cytherella* sp. Oertli, pls. XXXIII ; XXXIV ; XXXV.
1969 *Cytherella fullonica* Jones & Sherborn. Bate : 395, pl. 5, fig. 9; pl. 6, fig. 1.

MATERIAL. 238 valves and carapaces.

DISTRIBUTION. Occurring in the *coronatum* zone at Brora ; the *lamberti* zone at Staffin Bay, and in the *athleta* zone at Woodham brickpit Oxfordshire.

DIMENSIONS. OC–Call–Ba–77 ; *coronatum* zone Brora.

		Length	Height	Width
R.V.	HU.16.J.11	0·79	0·44	0·19
L.V.	Io.5036	0·72	0·38	0·16
Carapace	Io.5037	0·77	0·44	0·33

ONTOGENY. The adult and the four preceeding growth stages are recognized. Dimensions from sample OC–Call–Ba–77, *coronatum* zone Brora, are given below.

		Length	Mean	Height	Mean	L : H
Adult	6 R.V.	0·77–0·79	0·78	0·43–0·46	0·44	1·77 : 1
	6 L.V.	0·71–0·76	0·73	0·37–0·41	0·38	1·88 : 1
Penultimate	6 R.V.	0·60–0·64	0·62	0·35–0·37	0·36	1·70 : 1
Instar	6 L.V.	0·61–0·67	0·64	0·33–0·36	0·35	1·85 : 1
Antepenultimate	3 R.V.	0·54–0·56	0·55	0·31	0·31	1·78 : 1
Instar	2 L.V.	0·54–0·56	0·55	0·29–0·30	0·30	1·86 : 1
Antepenultimate	2 R.V.	0·49	0·49	0·29	0·29	1·70 : 1
Instar minus one	1 L.V.	0·47	0·47	0·27	0·27	1·74 : 1
Antepenultimate / Instar minus two	1 R.V.	0·36	0·36	0·23	0·23	1·57 : 1

Although insufficient of the earlier instars occur to give a good statistical sample, some interesting facts emerge. In the adult, both the length and height of the right valve is greater than the left. In the penultimate growth stage, the left valve is longer but less high than the right. In all cases the length : height ratio is greater in the left than in the right valve.

REMARKS. The species is very variable in shape and size. Specimens from the

coronatum zone of Brora are larger and proportionally higher than those from the *athleta* zone of Woodham ; those from the *athleta* zone of Staffin Bay have a more convex dorsal and a straighter ventral margin than those from Brora. These variations are here considered to be acceptable within the plexus of a single species.

The present material is rather larger, with minutely punctate shell surface, than that recorded by Bate (1963) from the Middle Bajocian Kirton Shale of Lincolnshire (L. 0·69–0·71 ; H. 0·35–0·39)

Suborder PODOCOPINA Sars 1866

Superfamily **BAIRDIACEA** Sars 1888

Family **MACROCYPRIDIDAE** Muller 1912

Genus ***MACROCYPRIS*** Brady 1867

Macrocypris aequabilis Oertli 1959

Plate 1. Figs. 17, 19, 21, 26.

1959 *Macrocypris aequabilis* n. sp. Oertli : 24, pl. 2, figs. 74–82.
1963 *Macrocypris* (*Macrocypris*) ? *aequabilis* Oertli 1959. Plumhoff : 18, pl. 1, figs. 4–8.
1964 *Macrocypris aequabilis* Oertli 1959. Glashoff : 30.

MATERIAL. 6 valves and carapaces.

DISTRIBUTION. Occurring in the *mariae* zone of Staffin Bay and Port-an-Righ and also in the *mariae* and *cordatum* zones in England.

DIMENSIONS. From sample OC–Ox–Pn–23, *mariae* zone, Purton brickpit, near Swindon, Wilts.

		Length	Height	Width
R.V.	Io.5038	0·36	0·16	0·08
Carapace	Io.5039	0·41	0·19	0·12

REMARKS. This species has been recorded from Britain before by Glashoff, 1964, from the *pseudocordata* zone of Yorkshire, and the *cymodoce* zone of Dorset. 10–12 anterior radial pore canals have been identified in the British material.

Subfamily **CYPRIDACEA** Baird 1845

Family **PARACYPRIDIDAE** Sars 1923

Genus **PARACYPRIS** 1866

Paracypris sp. A.

Plate 1. Figs. 20, 22, 23, 29.

MATERIAL. 49 valves and carapaces, mostly crushed and very poorly preserved.

DISTRIBUTION. Almost exclusively a Scottish species, occurring in the *coronatum* zone at Brora, the *mariae* zone at Port-an-Righ, and in the *lamberti* and *mariae* zones

at Staffin Bay. It also occurs in one sample from the *lamberti* zone of Tidmoor point, near Weymouth, Dorset.

DIMENSIONS. OC–Ox–SB–81, *mariae* zone Staffin Bay.

		Length	Height	Width
Carapace	HU.16.J.29	0·85	0·39	0·28

DESCRIPTION. Large, Slightly bow-shaped, elongate. Left valve considerably larger than right with overlap all round, strongest ventrally. Anterior margin rounded ; posterior acuminate with apex below mid-height. The dorsal margin is strongly arched ; ventral margin medianly concave. Greatest length just below mid-height ; greatest height and width antero-medianly. Valve surface minutely punctate. Anterior marginal area broad with a large vestibulum. Hinge simple with a narrow dorsal ridge in the right and a shallow complementary groove in the left valve.

REMARKS. This species is left with nomina aperta, because the poorly preserved nature of the material renders a complete description impossible. It differs from most other Jurassic members of the genus in being only slightly acuminate posteriorly and with the posterior apex only just below mid-height instead of being sub-ventral. It appears to be closest to *Paracypris* ? *sp. 2041*, described by Grekhoff (1963) from the Lower Callovian of Madagascar.

Family **PONTOCYPRIDIDAE** G. W. Müller 1894

Genus ***ARGILLOECIA*** Sars 1866

Argilloecia (?) sp. A.

Plate 1. Figs. 24, 25, 27, 28.

MATERIAL. One carapace from sample OC–Ox–P.a.R.–50a, *mariae* zone, Port-an-Righ.

DIMENSIONS.

		Length	Height	Width
Carapace	Io.5040	0·53	0·25	0·21

DESCRIPTION. Medium. Subrectangular, elongate. Left valve larger than right, with slight dorsal and very strong ventral overlap. Anterior margin well-rounded with extremity at mid-height. Dorsal margin arched ; ventral with slight median concavity. Cardinal angles prominent. Greatest length below mid-height ; height medially ; width postero-medianly. Valve surface minutely punctate. Muscle scars seen through the shell consist of a close group of 5 scars with three anteriorly and 2 behind.

REMARKS. Insufficient material requires that this species be left with open nomenclature. It differs from other species of *Argilloecia* in being less acuminate posteriorly, less arched dorsally, and in having the left valve rather than the right as the larger valve. However, because the muscle scar pattern is so similar to that of the type species of *Argilloecia*, the specimen is tentatively included in this genus.

Family **KRAUSELLIDAE** Berdan 1961

Genus ***KRAUSELLA*** Ulrich 1894

REMARKS. *Krausella* is here considered to belong to the Cypridacea and the monotypic family Krausellidae, rather than to the Healdicea of the Metacopina. This change of taxonomic position is based on the nature of the muscle scars which resemble more closely the cyprid than any other type. A substantiation of this change will be embodied in a later paper on the Oxfordian Ostracods of southern England in which a large fauna of *Krausella* will be described.

Krausella sp. A

Plate 2. Figs. 1, 2, 5, 6.

MATERIAL. 5 carapaces. From the coronatum zone of Brora, the *mariae* zone of Port-an-Righ, and also from the Corallian, *cautisnigrae* zone of the Dorset Coast.

DIMENSIONS. OC–Call–Ba–87. *coronatum* zone, Brora.

		Length	Height	Width
Carapace	Io.5041	0·54	0·27	0·25

DESCRIPTION. Medium. Elongate, oval. Pointed posteriorly. Elliptical in dorsal view. Left valve considerably larger than right with overlap all round except posteriorly where the strongly pointed posterior margin of the right valve projects beyond the left. Anterior margin narrowly rounded. Dorsal margin arched ; ventral margin gently convex. Greatest length just below mid-height ; greatest height and width median. Valve surface smooth. Internal features not seen.

REMARKS. This species differs from *K. argoviensis* Oertli 1959, in its smaller size and less rectangular outline.

Superfamily **CYTHERACEA** Baird

Family **SCHULERIDEIDAE** Mandelstam 1959

Subfamily **SCHULERIDEINAE** Mandelstam 1959

Genus ***PRAESCHULERIDEA*** Bate 1963

Praeschuleridea batei n. sp.

Plate 2. Figs. 3, 4, 9–22.

1960 Schuleridea sp. 1. Lutze : 434, pl. 37, figs. 6, 8.

DIAGNOSIS. *Praeschuleridea* with strongly pitted ornament ; pronounced sexual dimorphism ; and considerable overlap of left over right valve.

HOLOTYPE. One male right valve. HU.17.J.6. Sample OC–Call–Ba–77, *coronatum* zone, Brora.

DERIVATO NOMINIS. In honour of Dr. R. H. Bate of the British Museum (Nat. Hist.), the author of the genus, in recognition of his valuable contribution to our understanding of Jurassic ostracods.

MATERIAL. 343 valves and carapaces.

DISTRIBUTION. Ranging from the *macrocephalus* to the *lamberti* zone, and occurring from the coast of Dorset to east Sutherlandshire. In Scotland, it occurs in abundance in the *coronatum* zone of Brora. In England, it occurs at a number of localities, mostly in the south, but never in the same abundance as at Brora.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
Male R.V.	HU.17.J.6	0·77	0·40	0·19
PARATYPES From same sample				
Male R.V.	Io.5042	0·76	0·39	0·19
Male L.V.	Io.5043	0·79	0·45	0·21
Female R.V.	Io.5044	0·67	0·40	0·19
Female L.V.	Io.5045	0·72	0·45	0·21
Female Carapace	Io.5046	0·71	0·45	0·34
Male Carapace	Io.5047	0·83	0·44	0·35

DESCRIPTION. Medium to large. Sub-rectangular to sub-ovate. Left valve considerably larger than right with overlap all round. Both dorsal cardinal angles distinct in the right valve ; in the left, the anterior is rounded. Anterior margin well rounded in left valve ; in right valve with angle above mid-height. In both valves the anterior extremity is below mid-height. Posterior margin pointed, more so in right than in left valve ; postero-ventral slope convex ; postero-dorsal slope straight in left valve, slightly concave in right. Dorsal margin straight in right and convex in left, particularly in female valves which may be almost umbonate. Greatest height occurs medianly ; width postero-ventrally. Instars smooth. Adult strongly pitted on lateral surface. Marginal borders smooth and narrow. Normal pore canals fairly numerous. Marginal areas of medium width. Inner margin and line of concrescence coincide ventrally but diverge very slightly anteriorly and posteriorly. Radial pore canals fan shaped ; 12 antero-ventrally, the most dorsal of which are strongly upturned ; 5–7 posteriorly. Hinge paleohemimerodont (Bate 1963). In the right valve, the terminal elements are elongate dentate ridges with five smooth, evenly spaced teeth anteriorly and 6 posteriorly. The median element is a smooth narrow ridge which is lowest and narrowest medianly. This ridge is bounded dorsally by a narrow groove which is in turn bounded dorsally by the slightly overturned edge of the valve. The median element is negative in the sense that it does project the line of commissure when viewed dorsally. In the left valve the terminal loculate sockets are open distally and above the median element is a broad accommodation groove. Muscle scars consist of a vertical row of 4 adductors, with a large oval anterior and a smaller antero-ventral scar. Sexual dimorphism conspicuous, the male valves being longer, proportionally less high and more parallel-sided than the females.

Remarks. This species is very common in the Callovian of Britain and is almost certainly conspecific with *Schuleridea sp. 1.* described by Lutze (1960) from the *jason* zone of Hildersheim. It differs from *Praeschuleridea caudata* (Donze and Enay 1962), the only other known species from above the Bathonian, in its pitted ornament, larger size and less acuminate posterior. From the type, *P. subtrigona* (Jones and Sherborn 1888), it differs in its larger size, more pronounced sexual dimorphism and pitted ornament. It is considerably larger than either *P. lepida* or *P. wartae* Blaszyk 1967. *P. mediopunctata,* Dreyer 1967 is much smaller and more ovate.

Family **BYTHOCYTHERIDAE** Sars 1926

Genus ***MONOCERATINA*** Roth 1928

Monoceratina scrobiculata Triebel and Bartenstein 1938

Plate 3. Figs. 1–7, 9, 10.

1938 *Monoceratina scrobiculata* n. sp. Triebel and Bartenstein : 508–509, pl. 1, fig. 5, pl. 2, fig. 6.
1958 *Monoceratina scrobiculata* Triebel and Bartenstein 1938. Bizon : 23.
1959 *Monoceratina scrobiculata* Triebel and Bartenstein 1938. Oertli : 25, pl. 4, figs. 92–95.
1960 *Monoceratina cf. scrobiculata* Triebel and Bartenstein 1938. Lutze : 433, pl. 37, fig. 7.
1962 *Monoceratina scrobiculata* Triebel and Bartenstein 1938. Fischer : 335, pl. 19, figs. 10–12.
1963 *Monoceratina scrobiculata* Triebel and Bartenstein 1938. Oertli : pls. XXV, 2., XXXVI.
1964 *Monoceratina scrobiculata* Triebel and Bartenstein 1938. Glashoff : 37–38.
non 1963 *Monoceratina* sp. cf. *M. scrobiculata* Triebel and Bartenstein 1938. Bate, 1963a : 190, pl. 4, figs. 1–4.

Material. 456 valves and carapaces. Ranging from the *coronatum* to the *plicatilis* zone and occurring from Dorset to N.E. Scotland. In Scotland it occurs in the *coronatum* zone at Brora, the *mariae* zone at Port-an-Righ, and in the *lamberti* and *mariae* zones at Staffin Bay. The species is of widespread occurrence in England.

Dimensions. OC–Ox–Wm–1. From the *mariae* zone of Woodham brickpit.

		Length	Height	Width
R.V.	Io.5048	0·80	0·37	0·35
L.V.	Io.5049	0·70	0·35	0·28
Carapace	Io.5050	0·67	0·34	0·49

The dimension of width includes the spine.

Remarks. This species has been recorded twice before from this country, by Lutze, 1960 from the *athleta* zone of Crook Hill brickpit Dorset, and from the *mariae* zone of Woodham brickpit; and by Glashoff 1964 from the *cordatum* zone of Huntingdonshire and from the Dorset coast. The present record from the *plicatilis* zone of the Dorset zone, is the highest for the species.

Monoceratina stimulea (Schwager 1866)

Plate 3. Figs. 8, 11–17.

1866 *Cythereis stimulea* Schwager M.S., Oppel & Waagen : 276, fig. 1.
1938 *Monoceratina stimulea* (Schwager 1866) Triebel & Bartenstein 1938 : 505–506, pl. 1.
1960 *Monoceratina stimulea* (Schwager 1866) Fernet : pl. 2, figs. 8–9.
1962 *Monoceratina stimulea* (Schwager 1866) Fischer : 334, pl. 19, figs. 8–9.
? non 1959 *Monoceratina cf. stimulea* (Schwager 1866) Oertli : 27, pl. 4.
? non 1964 *Monoceratina cf. stimulea* (Schwager 1866) Glashoff : 38.

MATERIAL. 61 valves and carapaces. Occuring only in the *mariae* zone, from two localities, Port-an-Righ and Woodham, being more common at the latter.

DIMENSIONS. OC–Ox–Wm–3, the *mariae* zone Woodham brickpit.

		Length	Height	Width
R.V.	Io.5051	0·60	0·31	0·24
L.V.	Io.5052	0·60	0·32	0·23
Carapace	Io.5053	0·57	0·32	0·44

The dimension of width includes the spine.

DESCRIPTION. Medium. Subrectangular. Right valve slightly larger than left. Anterior margin well rounded with extremity at or just above mid-height ; posterior margin pointed sub-dorsally. Dorsal margin straight ; ventral margin posteriorly convex with a strong postero-ventral keel. Anterior cardinal angle more marked and more anterior in left than in right valve. Greatest height in posterior one third of valve ; width postero-ventrally. Valve surface smooth and shell thin and translucent. There is a prominent median sulcus and large ventro-laterally directed spine arising ventro-medianly. This spine is smooth except for annular costae and reticulae at its base. Marginal areas rather wide for the genus. Small vestibula at each end. Hinge adont, with a narrow smooth groove in the right valve, bounded dorsally and ventrally by smooth ridges and a complementary smooth bar in the left valve. The central muscle scars are situated on a median ridge, the internal reflection of the median sulcus, and consist of a crescentic line of five scars. Anterior scars not seen.

REMARKS. This is the first record of the species from Britain. Oertli's 1959 record of *M.* cf. *stimulea* would seem to be better considered as *M. vulsa* (Jones & Sherborn) : and similarly the record from the Yorkshire *cautisnigrae* (Glashoff 1964) since although not figured, he remarks on the similarity of this to Oertli's 1959 material.

Monoceratina vulsa (Jones & Sherborn 1888)

Plate 3. Figs. 18–25.

1888 *Cytheridea vulsa* Jones & Sherborn : 263, pl. 2, fig. 4.
1938 *Monoceratina vulsa* (Jones & Sherborn 1888). Triebel & Bartenstein : 516, pl. 3, figs. 17–18.
? 1959 *Monoceratina cf. stimulea* (Schwager 1866). Oertli : 27, pl. 4, figs. 96–97.
1960 *Monoceratina cf. vulsa* (Jones & Sherborn 1888). Lutze : 433, pl. 37, fig. 5.

1963 *Monoceratina* sp. juv. aff. *vulsa* (Jones & Sherborn 1888). Plumhoff : 48, pl. 11, figs. 167–168.
1963 *Monoceratina vulsa* (Jones & Sherborn 1888). Bate (1963b) 26, pl. 1, fig. 6.
1963 *Monoceratina vulsa* (Jones & Sherborn 1888). Oertli : XXXII, 2.
1964 *Monoceratina vulsa* (Jones & Sherborn 1888). Bate : 9.
? 1964 *Monoceratina cf. stimulea* (Schwager 1866). Oertli 1959. Glashoff : 38.
1967 *Monoceratina cf. vulsa* (Jones & Sherborn 1888). Blaszyk : 68, 69. pl. 10, fig. 4.
1969 *Monoceratina vulsa* (Jones & Sherborn). Bate : 400 and 401, pl. 7, fig. 5.

MATERIAL. 122 valves and carapaces. Occurring widely throughout Britain and ranging from the *macrocephalus* to the *plicatilis* zones, being most abundant in the *athleta* zone. In Scotland it occurs in the *mariae* zone at Port-an-Righ, and in the same zone at Staffin Bay.

DIMENSIONS. OC–Call–Wm–24, *athleta* zone, Woodham.

		Length	Height	Width
R.V.	Io.5054	0·64	0·29	0·16
L.V.	Io.5055	0·63	0·28	0·15
Carapace	Io.5056	0·65	0·29	0·27

REMARKS. This species is similar in shape and size to *M. ungulina* Triebel & Bartenstein 1938, but differs in being ornamented, the latter being smooth. Although very little variation is shown throughout the range of the present material, there is a tendency for later forms to be less ornamented than those from lower horizons. None of the present specimens are as strongly pitted as the type material.

Monoceratina sp. A.

Plate 3. Fig. 26.

MATERIAL. 3 broken valves. From Sample OC–Call–SB–71 *lamberti* zone, Staffin Bay.

REMARKS. These specimens are very similar to *M. vulsa* (Jones & Sherborn), but differ in possessing 4 strong marginal spines at the anterior cardinal angle. A number of very narrow radial pore canals are seen anteriorly, where there is a strong vestibule. This would appear to be a new form, perhaps a subspecies of *M. vulsa*. It is left with open nomenclature at present because of inadequate material.

Family **CYTHERIDEIDAE** Sars 1925

Subfamily **CYTHERIDEINAE** Sars 1925

Genus ***GALLIAECYTHERIDEA*** Oertli 1957

Galliaecytheridea staffinensis n. sp.

Plate 4. Figs. 1–6.

DIAGNOSIS. *Galliaecytheridea* with thick shell and strongly pitted and punctate ornament. Posterior cardinal angle distinct ; posterior margin pointed at mid-height. Strongly inflated medianly and with left valve strongly overlapping right.

HOLOTYPE. One carapace HU.18.J.8, sample OC–Ox.SB.94, *cordatum* zone, Staffin Bay, to which locality and zone, the species would appear to be restricted.

MATERIAL. 20 valves and carapaces.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
Carapace	HU.18.J.8	0·77	0·51	0·36
PARATYPE	From same sample.			
Carapace	Io.5058	0·80	0·51	0·35

DESCRIPTION. Large. Subrectangular to subquadrate. Mean length : height ratio 1·59 : 1. Elliptical in dorsal view, end margins laterally compressed particularly anteriorly. Left valve larger than right with conspicuous overlap. Anterior margin well-rounded; posterior pointed at mid-height, with a convex postero-ventral and a straight or slightly concave postero-dorsal slope. Anterior cardinal angle rounded ; posterior distinct. Dorsal margin short and slightly concave, ventral margin gently convex, upturned posteriorly. Greatest length at mid-height ; height, at the anterior cardinal angle ; width, postero-median. Valve surface pitted to punctate with smooth marginal borders and strong antero-marginal furrow. Normal pores large and fairly numerous. Marginal areas rather narrow ; line of concrescence and inner margin coincident throughout. Radial pore canals short and straight with 12–14 anteriorly and 4 posteriorly. Hinge hemimerodont, only seen in fragmentary valves. In the left valve, the anterior terminal element is a loculate socket with 5 locules, which is overhung dorsally and open both proximally and distally. No other part of the hinge seen, except for a small part of the median element, a smooth bar. Muscle scars a vertical line of four adductors with a heart-shaped anterior and a smaller antero-ventral scar.

REMARKS. This species most closely resembles *G. wolburgi* (Steghaus 1951), but differs in being more heavily ornamented, more parallel sided and inflated.

Genus ***GLABELLACYTHERE*** Wienholz 1967

Glabellacythere reticulata n. sp.

Plate 4. Figs. 7–15, Plate 5, Figs. 1–6.

1962 Ostracod No. 138 Brand. Brand and Fahrion : 153, pl. 21. figs. 37–38.

DIAGNOSIS. *Glabellacythere* characterized by the possession of strongly reticulate ornament and very pronounced sexual dimorphium.

HOLOTYPE. One female carapace, HU.18.J.11, from sample OC–Call–Sb–72, *lamberti* zone Staffin Bay, Isle of Skye.

DERIVATO NOMINIS. From the reticulate nature of the ornament.

MATERIAL. 72 valves and carapaces.

DISTRIBUTION. Wide spread in the Callovian of southern England and in Scotland occurring in the *coranatum* zone Brora and in the *lamberti*, *mariae* and *cordatum* zones of Staffin Bay.

DIMENSIONS. Sample OC–Call–SB–72, *lamberti* zone, Staffin Bay.

		Length	Height	Width
HOLOTYPE				
Female Carapace	HU.18.J.11	0·67	0·35	0·39
PARATYPES	Same sample as holotype.			
Female R.V.	Io.5060	0·67	0·35	0·20
Female L.V.	Io.5061	0·67	0·36	0·21
Male R.V.	Io.5062	0·77	0·34	0·21
Male L.V.	Io.5063	0·80	0·35	0·21
Male carapace	Io.5064	0·76	0·33	0·35

DESCRIPTION. Medium to large. Sub-rectangular. Strongly inflated postero-medianly, laterally compressed at each end. Left valve larger than right with overlap at the cardinal angles. Cardinal angles both angular in the left valve ; in the right, particularly males, the posterior cardinal angle is more rounded. Anterior margin rounded in right valves ; more angular in left. Extremity below mid-height. Posterior margin bluntly pointed in left valve ; more pointed in right with a convex postero-ventral and a concave postero-dorsal slope. Dorsal margin slightly concave medianly with a small anterior hinge ear ; ventral margin with slight median concavity. These margins sub-parallel, particularly in male valves. Greatest length at mid-height ; height at the anterior cardinal angle ; width in posterior third. Marginal borders smooth. Lateral surface coarsely reticulate. Ventrally, the ridges whose ramifications give rise to the reticulations, become aligned parallel to the ventral margin as a series of weak ridges. A flange frill borders the anterior margin. Eye spot small, better developed in right than left valve. Normal pores few. Marginal areas of medium width, small vestibula occur at each end. Radial pore canals thin, straight and widely spaced ; 6 anteriorly and 3–4 posteriorly. Hinge antimerodont. In the right valve the terminal elements are raised dentate ridges with 5 teeth anteriorly and 6 or 7 posteriorly. The median element is a locellate groove ; open ventrally and closed dorsally by a ridge which itself contains a shallow groove. Complementary structures occur in the left valve hinge where the terminal elements are open distally. A weak shelf-like accommodation groove occurs above the hinge in the left valve. Muscle scars consist of 4 equal sized adductors in a vertical line, and a large oval anterior and smaller antero-ventral sear. Sexual dimorphism strongly pronounced, the males being longer and proportionally less high than the females.

REMARKS. This species differs from *G. dolabra* (Jones & Sherborn) in its strongly developed ornament and sexual dimorphism.

Glabellacythere dolabra (Jones & Sherborn)

Plate 5. Figs. 7–18.

1888 *Cytheridea dolabra* Jones & Sherborn : 267, pl. 3, figs. 3a-c.
1888 *Cytheridea puteolata* Jones & Sherborn : 259, pl. 1, figs. 7a-c.
1888 *Cytheridea parallela* Jones & Sherborn : 260, pl. 1, figs. 9a-c.
1888 *Cytheridea pentagonalis* Jones & Sherborn : 261, pl. 2, figs. 1a-c.
1888 ?*Cytheridea ignobilis* Jones & Sherborn : 268, pl. 3, figs. 9a-c.
1967 *Glabellacythere nuda* n. sp. Wienholz : 31, pl. 3, figs. 32–34 ; pl. 4, fig. 35.
1969 *Hadrocytheridea dolabra* (Jones & Sherborn) Bate : 407–409, pl. 9, figs. 1–8, pl. 10, fig. 1 ; Text-fig. 7.

MATERIAL. 112 valves and carapaces.

DISTRIBUTION. Occurring from Dorset to Skye and ranging from the *macrocephalus* to the *cordatum* zone. In Scotland, occurring in the *lamberti* zone of Staffin Bay.

DIMENSIONS. From Sample OC–Call–CH–14, *athleta* zone, Crook Hill.

		Length	Height	Width
Female R.V.	Io.5065	0·64	0·35	0·20
R.V.	HU.18.J.18	0·67	0·35	0·20
L.V.	Io.5066	0·67	0·37	0·20
Carapace	Io.5067	0·65	0·37	0·33

REMARKS. Sexual dimorphism, rarely expressed, is confined to the presence of a few broken male valves, found in the earlier part of the range of the species. The presence of small vestibula in this material contrasts it with the Bathonian species. Instars are rare amongst the Scottish material, and the ontogeny of *G. dolabra* will be discussed in a later paper in which the English Ostracoda of this age are described. This species bears a strong external, but entirely superficial resemblance to *Dolocythere maculosa* Bate. Bate (1969) erected the genus *Hadrocytheridea* to accommodate this species and earlier Wienholz (1967) had erected the genus *Glabellacythere* based upon the same species which she called *nuda*[1]. The present author has followed Bate in assigning this species to the *Cytherideinae* rather than the *Progonocytherinae* as favoured by Wienholz.

Family **CYTHERURIDAE** G. W. Müller 1894

Genus ***PROCYTHERURA*** n. gen.

TYPE SPECIES. *Procytherura tenuicostata* n. sp.

DIAGNOSIS. Similar in shape to *Cytherura* Sars. Small. Valves subequal, right slightly higher than left. Weakly sulcate antero-medianly. Ornament variable from almost smooth to wrinkled or costate. Radial canals straight and thin, thickened proximally. Hinge lophodont, the terminal elements in the right valve being smooth narrow ridges. Eye spot weak. Narrow vestibula occur at each end. Muscle scars of 4 adductors with a single large heart-shaped anterior scar.

[1] See Addendum

REMARKS. *Procytherura* is considered to be ancestral to *Cytherura* Sars. The shape of the two genera is very similar and in both the right valve overhangs the left dorsally. The main differences are in the hingement, muscle scars and marginal areas. In *Cytherura*, the hinge is " hemimerodont ", in *Procytherura* it is lophodont. Vestibula are absent in *Cytherura* and prominent in *Procytherura* ; in the former the anterior scars consist of an oval scar with an oblique elongate scar and a smaller circular scar anterior to it, in the latter there is a single heart-shaped anterior scar. From *Vesticytherura* Grundel, this genus differs in shape ornament and hingement. Of the species described as *Cytherura* by Oertli (1957, 1959), from the Upper Oxfordian of France and Switzerland, none would appear to belong to *Procytherura*. Dr. Oertli has been kind enough to send specimens of most of these, and *C.* ? *lacrimula* and *C. liesbergensis* certainly do not belong here, but probably to a new genus within the family. *Monoceratina sundancensis* Swain and Peterson 1951, may belong in *Procytherura*, as its shape and ornament are very similar. *Cytherura bathonica* and *C. mediojurassica* Bate 1969 may well belong to *Procytherura* but as they are only known as carapaces it is not possible to be certain.

Procytherura tenuicostata n. sp.

Plate 6. Figs. 1–8. Text fig. 6 a-d.

DIAGNOSIS. *Procytherura*, with shape and ornament very similar to the type of *Cytherura*. Hinge lophodont and weakly developed. Vestibula at each end. Muscle scars a vertical line of 4 adductors with a single heart-shaped anterior scar.

HOLOTYPE. One left valve HU.18.J.30. Sample COR–DC–16, top of Nothe Clay, *plicatilis* zone, Corallian of the Dorset Coast.

DERIVATO NOMINIS. From the weakly ornamented nature of the carapace.

MATERIAL. 114 valves and carapaces.

DISTRIBUTION. Widespread throughout the English Oxfordian, ranging from the *mariae* to the *pseudocordata* zone. In Scotland it occurs in the *plicatilis* zone at Port-an-Righ.

DIMENSIONS

		Length	Height	Width
HOLOTYPE				
L.V.	HU.18.J.30	0·39	0·16	0·10
PARATYPES	Same sample as holotype.			
		Length	Height	Width
R.V.	Io.5068	0·36	0·16	0·10
R.V.	Io.5069	0·36	0·16	0·10
L.V.	Io.5070	0·35	0·19	0·10
Carapace [specimen lost]	HU.18.J.34	0·36	0·20	0·16

DESCRIPTION. Very small, thin-shelled. Subrectangular, elongate. Valves subequal, right overeaching left dorsally. Slightly bilobed in dorsal view due to weak median sulcus. Anterior margin rounded ; posterior produced into a caudal process with a blunt apex above mid-height. Dorsal margin straight, anterior cardinal angle slightly more prominent in left than in right valve. Ventral margin with shallow median concavity and well-developed postero-ventral keel, especially in right valve. Greatest length above mid-height ; height at the anterior cardinal angle ; width in posterior third. Ornament variable from smooth to wrinkled or weakly reticulate. Normal pore canals few, small and widely spaced. Eye spot small and not prominent. Marginal areas of variable width, narrow vestibula occur at each end. Selvage strongly developed ventrally and flange anteriorly. Radial pore canals straight, thin with proximal thickening, 5 anteriorly, 2–3 posteriorly. Hinge lophodont with weak terminal elements. In the right valve, the median element is a shallow smooth to feebly locellate groove which widens distally and which passes dorsal to the proximal parts of the terminal elements which are low weak smooth ridges. The groove is bounded dorsally by the edge of the valve and is open ventrally in its mid-part. Complementary structures occur in the left valve, where a weak shelf-like accommodation groove may be present. Muscle scars consist of a subcentral line of 4 adductors, with a large heart-shaped anterior scar.

REMARKS. The amount of variation in the ornament exhibited by this species is considerable. Some forms are smooth, others weakly reticulate. There appears to be no trend associated with this variation which occurs in any population at any horizon. A further species of this genus, from the Callovian of Dorset will be described in a later paper. *P. tenuicostata* differs from both *Cytherura bathonica* and *C. mediojurassica* Bate in its weaker ornament.

Genus ***EUCYTHERURA*** G. W. Müller 1894

Subgenus ***VESTICYTHERURA*** Gründel 1964

Eucytherura (Vesticytherura) costaeirregularis n. sp.

Plate 6. Figs. 9–19, 21.

DIAGNOSIS. *Vesticytherura* with ornament of impersistant and irregular ribs and variable intervening reticulae. Eye tubercule rib biramous. Median and dorsal ribs either main separate or only tenuously linked posteriorly.

HOLOTYPE. One left valve HU.18.J.40 from sample AC–Mel–5, 5 feet below the main stone band, Ampthill Clay, *cautisnigrae* zone, Melton, Yorks.

DERIVATO NOMINIS. From the irregular expression of the ribs.

MATERIAL. 189 valves and carapaces.

DISTRIBUTION. Occurring in the *coronatum* zone of Brora, the *lamberti* and *mariae* zones of Staffin Bay and the *mariae* zone of Port-an-Righ, and widely distributed between the *macrocephalus* and *plicatilis* zones in England.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
L.V.	HU.18.J.40	0·35	0·21	0·11
		Length	Height	Width
PARATYPES.	Same sample as holotype.			
R.V.	Io.5071	0·35	0·18	0·09
L.V.	Io.5072	0·36	0·21	0·10
L.V.	Io.5073	0·34	0·20	0·10
R.V.	Io.5074	0·36	0·19	0·09
Carapace	Io.5075	0·35	0·21	0·17

DESCRIPTION. Very small. Subquadrate to subrectangular. Slightly bilobate in dorsal view due to the possession of a weak antero-median sulcus. Left valve larger than right with slight dorsal overlap. Anterior margin of right valve rounded, that of left more angular. Anterior cardinal angle stronger and more anterior in left than in right valves. Posterior margin produced into a sub-dorsal caudal process with a rather blunt apex. Dorsal margin straight in left and slightly convex in right valves. Ventral margin straight, strongly upturned posteriorly. Greatest height at the anterior cardinal angle ; length, sub-dorsally ; width, in the posterior third.

Surface ornament of rather weak, impersistant and irregular ribs with very variable intercostate ornament. There are two short ventral ribs. From a postero-ventral prominence, a short rib extend antero-ventrally for a short distance before changing direction antero-dorsally to its termination, ventral to an antero-median position. This rib is rather variable, but its overall ' V ' shape is characteristic of the species. A weak and very variable median rib occurs, which may or may not be joined by a dorsal extension, to the dorsal rib. In some cases this rib may be terminated medianly, in others it may extend onto the anterior marginal border. The dorsal rib extends from a postero-dorsal position, along the dorsal margin, and may be terminated either anterior or posterior to the eye tubercule. The eye turbercule is circular, glassy and prominent. From it a short rib extends antero-ventrally to the marginal border, and another ventrally which may or may not join the median rib. A variable number of small irregular ribs also occur. The intercostate areas vary from reticulate to almost smooth. Three large tubercules occur at the base of the caudal process and a large number of small tubercules occur randomly. Five strong marginal denticles occur anteriorly. Normal pores few, large and well spaced. Marginal areas wide. Large vestibula occur at each end. Radial pores slightly sinuous, widely spaced and thickened proximally; 5 anteriorly and 3–5 posteriorly. Hinge with right valve terminal elements consisting of a single smooth circular or oval tooth at each end, connected by a locellate groove. Complementary structures occur in the left valve hinge, above which is a shelf-like accommodation groove. There are four vertically aligned adductor scars and a large oval anterior scar.

REMARKS. This species is most closely related to *E.* (*V.*) *gruendeli* (n. sp. in press) which occurs widely in the English Oxfordian and which will be described in a later work.

Eucytherura (Vesticytherura) horrida n. sp.

Plate 6. Figs. 20, 22–24, Plate 7, Figs. 1–6.

DIAGNOSIS. A new species of *Vesticytherura* whose ornament is the product of an interaction of coarse irregular ribs and tuberules.

HOLOTYPE. One left valve, HU.18.J.50, sample OC–Ox–Wm–1, *mariae* zone three feet above the base, Woodham brickpit, Oxfordshire.

DERIVATO NOMINIS. L. rough ; pertaining to the rough tuberculate and spinose nature of the surface ornament.

MATERIAL. 21, valves and carapaces.

DISTRIBUTION. Occurring in the *lamberti* and *mariae* zones of Staffin Bay, and in England at similar levels.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
L.V.	HU.18.J.50	0·36	0·20	0·12
PARATYPES	Same sample as holotype.			
L.V.	Io.5076	0·35	0·20	0·09
R.V.	Io.5077	0·36	0·21	0·12
Carapace	Io.5078	0·35	0·19	0·19

DESCRIPTION. Very small. Subquadrate. Left valve slightly larger than right with dorsal overlap. Slight median sulcus. Anterior margin rounded ; posterior margin produced into a caudal process with apex at mid-height and with convex postero-ventral and concave postero-dorsal slope. Dorsal margin straight, ventral margin with slight median concavity. Greatest length above mid-height ; height, at the anterior cardinal angle ; width, postero-ventrally. Ornament consisting of irregular ribs, tubercules and reticulations. An elevated alate prominence, surmounted by an irregular tubercule, occurs postero-ventrally. A similar feature occurs postero-dorsally and overhangs the dorsal margin, in some cases being produced into a dorsal rib. An irregular postero-median tubercule is developed in some specimens. The eye spot is surmounted by an irregular rib which may extend beyond the dorsal margin. A weak ventral rib occurs. The remainder of the valve surface is reticulate and irregularly tuberculate. Five or six strong marginal denticles occur anteriorly. Marginal areas wide with vestibula at each end. Radial pore canals thickened proximally ; 5 anteriorly and 2 posteriorly. Hinge of right consists of a single smooth terminal tooth at each end, connected by a locellate groove. Complementary structures occur in the left valve hinge, above which is a weak, shelf-like accommodation groove. There are four vertically disposed adductors and a single oval anterior sear.

REMARKS. This species differs from others of the genus in the irregular and tuberculate nature of the ornament. It is rather larger and lacks the prominent mid-dorsal tubercule of *E.* (*V.*) *multituberculata* Gründel 1964, from the German Albian. The species forms a useful marker for the *lamberti* and the lower part of the *mariae* zones.

Eucytherura (Vesticytherura) scottia n. sp.

Plate 7. Figs. 7–13.

DIAGNOSIS. A new species of *Vesticytherura* with ornament of broad smooth ribs and low smooth tubercules. Intercostate areas smooth or weakly reticulate.

HOLOTYPE. One left valve, HU.18.J.36, sample OC–Ox–SB–87, *cordatum* zone, Staffin Bay.

DERIVATO NOMINIS. L. From the apparent restriction of the species to the Jurassic of Scotland.

MATERIAL. 28 valves and carapaces.

DISTRIBUTION. Occurring in the *coronatum* zone of Brora, and the *mariae* and *cordatum* zones of Staffin Bay.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
L.V.	HU.18.J.37	0·39	0·21	0·11
PARATYPES	Sample OC–Call–Ba–86, *coronatum* zone, Brora.			
Carapace	Io.5079	0·39	0·22	0·17
Carapace	Io.5080	0·37	0·22	0·16

DESCRIPTION. Very small. Subquadrate to subrectangular. Left valve slightly larger than right with dorsal overlap. Anterior margin poorly rounded with extremity below mid-height ; posterior margin pointed in right and bluntly rounded in left, apex above mid-height. Posterior cardinal angle pronounced in both valves ; anterior more rounded in right than left. Dorsal margin with slight median convexity; ventral medianly straight, upturned posteriorly. Greatest height at the cardinal angles ; width, postero-ventrally ; length, above mid-height. Ornament variable, consisting of a series of broad longitudinal ribs and swellings, and with either smooth or reticulate intervening areas. A broad, posteriorly alate rib, extends from a postero-ventral position across the ventro-lateral surface of the valve, terminating antero-ventrally. A similar broad, rib, which is broken mid-dorsally, extends along the dorso-lateral surface. The eye tubercule is well developed and is connected to a large smooth mid-anterior tubercule by a short rib. A further tubercule occurs ventral to the latter. Intercostate areas are variable smooth or reticulate. Small marginal denticles occur anteriorly. Normal pores few and widely spaced. Marginal areas wide, with large vestibula at each end. Radial canals thickened proximally ; 5 anteriorly and 2 posteriorly, the latter may branch. Flange well developed anteriorly. Right valve hinge consisting of two small oval terminal teeth connected by a finely locellate groove, with complementary structures in the left valve. There is no accommodation groove.

REMARKS. This species most closely resembles *Eucytherura ansata* Weingeist 1949, from the American Cretaceous, but differs in possessing a dorsal rib, rather than three isolated dorsal tubercules.

Genus *CYTHEROPTERON* Sars 1866

Cytheropteron aquitanum Donze 1960

Plate 7. Figs. 14–16.

1960 *Cytheropteron aquitanum* n. sp. Donze, 21–22, pl. 4, figs. 48–51.
1963 *Eocytheropteron aquitanum* (Donze 1960). Oertli, pl. XLVIII.
1969 *Cytheropteron aquitanum* Donze, Kilenyi : 141, pl. 28, figs. 8–11.

MATERIAL. One complete left valve and three fragments.

DISTRIBUTION. From the *coronatum* zone of Brora, and also from the *plicatilis* zone of Dorset.

DIMENSIONS. *plicatilis, Dorset,* sample COR–DC–7.

		Length	Height
L.V.	Io.5081	0·43	0·28

REMARKS. The small size of the present specimens is probably attributable to their being growth stages, the length of the holotype being 0·57. The two previous records are from the Kimmeridgian, and the present record is an extension of the range and the first record of the species from Britain. The single complete specimen from the *plicatilis* zone of Dorset seem to be an undoubted member of the species. The broken nature of the Scottish Callovian specimens, however, makes their correct identification somewhat conjectural. The species is returned to the genus *Cytheropteron* from *Eocytheropteron* as its hinge is more typical of the former as also is its alar development.

Genus *METACYTHEROPTERON* Oertli 1957

Metacytheropteron sutherlandensis n. sp.

Plate 7. Figs. 17–24.

DIAGNOSIS. *Metacytheropteron* with left valve longer than right. Ventral part of anterior margin rounded, projecting below ventral margin. Ornament of weak reticulations is longitudinally aligned. Weak eye tubercule and furrow in left valve. Hinge weak, antimerodont. Dimorphic.

HOLOTYPE. One male right valve, HU.19.J.12. Sample OC–Call–Ba–86. *coronatum* zone Brora.

DERIVATO NOMINIS. After the county of Sutherlandshire, to the Callovian shales of which the species is apparently restricted.

MATERIAL. 69 valves.

DISTRIBUTION. Occuring in 8 samples, all from the Fascally brickpit at Brora, *coronatum* zone.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
Male R.V.	HU.19.J.12	0·55	0·27	0·16
PARATYPES	Same sample as holotype.			
Male L.V.	Io.5082	0·55	0·26	0·16
Female L.V.	Io.5083	0·46	0·25	0·15

DESCRIPTION. Medium. Subrectangular, elongate. Thin-shelled. Dimorphic. Inflated postero-ventrally. Anterior margin straight antero-dorsally, rounded antero-ventrally and extending below the ventral margin, with extremity below mid-height. Posterior margin bluntly pointed with apex at mid-height. Dorsal margin straight ; ventral medianly obscured by valve tumidity. Male valves more parallel-sided and less posteriorly convergent than females. Greatest length at mid-height ; height, at anterior cardinal angle ; width, in posterior third. Ornament of weak reticulations, the weak ridges which extend from these being longitudinally aligned dorso and ventro-laterally. Anteriorly there is a convergence of these ridges which meet at about mid-height. The extreme marginal borders are smooth. In the left valve, there is a weak eye tubercule with an oblique furrow behind it. Flange frill-like anteriorly. Normal pores few, large and widely spaced. Marginal areas very narrow. Line of concrescence and inner margin coincide throughout. Hinge antimerodont, feebly developed. In the right valve the terminal elements are very low and consist anteriorly of five small oval teeth with five of six posteriorly. The median element is a locellate groove, partly open ventrally and closed dorsally by the edge of the valve. Complementary structures occur in the left valve hinge, above which is a gutter-like accommodation groove. Muscle scars not seen. Sexual dimorphism pronounced, the males being larger, longer, and more parallel-sided than the females.

REMARKS. This species differs from the type, *M. elegans* Oertli from the French Kimmeridgian, in its smaller size, weaker and less longitudinally aligned ornament and in its weaker hinge. From *M. ? striatulum* Anderson 1964, this species differs in being more elongate and parallel-sided and in possessing a much less prominent anterior cardinal angle. *M. nannodes* Anderson 1964, from the Rhaetic, would appear from its very small size to belong to *Procytherura* n. gen., but as the original description does not mention internal features, it is not possible to be certain.

Metacytheropteron sp. A.

Plate 8. Figs. 1–4.

MATERIAL. 3 carapaces and one broken valve.

DISTRIBUTION. Found only in the *coronatum* zone at Brora.

DIMENSIONS. Sample OC–Call–Ba–76

		Length	Height	Width
Carapace	Io.5084	0·44	0·20	0·19

DESCRIPTION. Small. Subrectangular. Left valve slightly larger than right with greatest overlap ventrally. The right valve is slightly longer than the left and projects beyond it anteriorly. Anterior margin broadly rounded, most sharply antero-ventrally where it projects below the ventral margin. Posterior margin bluntly pointed at mid-height. Dorsal margin with slight median convexity ; ventral margin concave. Surface sculpture of 8–10 longitudinal costae extending the length of the carapace, the most dorsal changing direction antero-ventrally in the anterior half of their extent. Internal features not seen.

REMARKS. This species differs from *M. sutherlandensis* n. sp. in being smaller and less inflated and in its much stronger costae. Insufficiency of material requires that the species be left with open nomenclature.

Genus ***PEDICYTHERE*** Eagar 1965

Pedicythere anterodentina n. sp.

Plate 8. Figs. 5–14.

DIAGNOSIS. *Pedicythere* with small circular terminal tooth in right valve. Ventro-lateral spine triangular in section with a sharp anterior leading edge and small secondary spines on the posterior. There is a strong postero-ventral marginal spine.

HOLOTYPE. One right valve HU.17.J.41 sample OC–Ox–wm–1, from the *mariae* zone of Woodham brickpit.

DERIVATO NOMINIS. Pertaining to the single anterior terminal tooth in the right valve.

MATERIAL. 15 valves and carapaces.

DISTRIBUTION. Occurring in the *mariae* zone of Port-an-Righ, and in the English *lamberti* and *mariae* zones.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
R.V.	HU.17.J.41	0·35	0·17	0·15
PARATYPES	Same sample as holotype.			
L.V.	Io.5085	0·36	0·17	0·20
R.V.	Io.5086	0·33	0·16	0·16
Carapace	Io.5087	0·32	0·16	0·29

The dimension of width includes the spine.

DESCRIPTION. Very small. Subquadrate with a strong ventro-lateral spine. Left valve slightly larger than right. Dorsal and ventral cardinal angles well marked anteriorly. Posterior margin produced into a slightly upturned caudal process, the apex of which may extend above the dorsal margin. Dorsal margin straight or slightly sinuous. Ventral margin straight, upturned posteriorly. There is a slight median sulcus. Greatest length dorsally; height, at the anterior cardinal angle ; width, postero-ventrally. Valve surface smooth or minutely punctate. There is a

large ventro-lateral spine which is triangular in section, the anterior leading edge being sharp and the posterior being blunter and often bearing small, backward directed secondary spines. The length of the spine is 0·10. A strong rib extends along the dorsal margin and its anterior termination is marked by a round tubercule which may or may not be visual in function. A number of small tubercules occur along the anterior margin, which may also bear marginal denticulations. There is a conspicuous postero-ventral spine. Marginal areas wide, with narrow vestibula at each end. A number of long thin radial canals occur anteriorly. The hinge in the right valve consists of a long straight smooth furrow with a single anterior terminal tooth, the posterior terminal element being absent. Complementary structures occur in the left valve hinge above which is a shelf-like accommodation groove.

Remarks. This species is placed in *Pedicythere* because of the great similarity in shape, size, ornament etc. It differs from the type, *P. tessae*, from the Lower Eocene London Clay, only in lacking a posterior terminal hinge element, *P. anterodentina* is thought to be an early ancestral form of the genus.

Family **PROGONOCYTHERIDAE** Sylvester-Bradley 1948

Subfamily **PROGONOCYTHERINAE** Sylvester-Bradley 1948

Genus ***CAYTONIDEA*** Bate 1965

Caytonidea terraefullonicae (Jones & Sherborn 1888)

Plate 2. Figs. 7, 8.

1885 *Cytheridea perforata* Terquem (Non Roemer) : 28, pl. lv, fig. 8.
1888 *Cytheridea terrae-fullonicae* sp. n. Jones & Sherborn : 258, pl. 1, fig. 5.
1969 *Caytonidea terrae-fullonicae* Jones & Sherborn; Bate : 410, pl. 10, figs. 2, 7, 8, pl. 11, figs. 1–3.

Material. 8 valves, mostly fragmentary. In Scotland occurring in the *coronatum* zone of Brora and in England in the Upper Cornbrash *macrocephalus* zone of Dorset and the *athleta* zone of Woodham brickpit.

Dimensions. OC–Call–Ba–78, Brora.

		Length	Height	Width
L.V.	Io.5088	0·61	0·32	0·20

Remarks. The author has seen the original material in the British Museum, which is identical to the specimens here described. This is the first record of the species from above the Bathonian.

Genus ***LOPHOCYTHERE*** Sylvester-Bradley 1948

Remarks. Subsequent to the original erection of the genus, a large number of species have been described. On grounds of ornament, these seem to fall into two distinct groups. On this basis, it is considered necessary and valuable to here subdivide the genus. The type species, *Lophocythere ostreata* (Jones & Sherborn), has an

ornament which consists of a strong ventral rib and a strong ventro-lateral rib which changes direction through 90 degrees antero-ventrally and extends to the eye tubercule. The valve surface dorsal to this rib is often strongly reticulate and bears a number of short thin ribs. The ornament is always the same in each valve. Species with this type of ornament, which include *L. scabra* s.l. Triebel 1951, are here retained as *Lophocythere*, subgenus (*Lophocythere*). Other forms, typified by *Lophocythere bradiana* (Jones), have an ornament consisting essentially of longitudinal ribs, usually 3 or 4 in number. The species of this second group lack the subvertical rib extending from the eye tubercule, and the details of ornament of the two valves often differs. Those species belonging to this group, the majority, are placed in the new subgenus, *Lophocythere* (*Neurocythere*).

Subgenus ***LOPHOCYTHERE*** Sylvester-Bradley 1948

EMENDED DIAGNOSIS. Subgenus of *Lophocythere* characterised by strong ventro-lateral rib which antero-ventrally changes direction through 90 degrees to extend to eye tubercule. Valve surface reticulate, tuberculate or spinose.

TYPE SPECIES. *Cytheridea ostreata* Jones and Sherborn 1888.

DESCRIPTION. Carapace medium to large. Subrectangular, parallel-sided with little posterior convergence. Left valve larger than right with strong dorsal overlap. Anterior margin rounded, usually with prominent frill-like flange. Posterior margin pointed in the region of mid-height, right valves usually more sharply than left. Dorsal margin straight or slightly concave medianly, cardinal angles distinct. Ventral margin straight or medianly concave, usually overhung by the ventral rib. Greatest length at, or near mid-height, greatest height at the anterior cardinal angle, greatest width in the posterior third. Valve surface strongly ornamented. There is a ventral rib which usually reaches the anterior margin. Above this is a strong vento-lateral rib extending across the valve from a postero-ventral to an antero-ventral position where it changes direction through 90 degrees, and extends dorsally to the eye tubercule. The ventro-lateral part of this rib may be discontinuous and spinose or tuberculate (*Lophocythere* (*L.*) *scabra bucki* Lutze). The remainder of the lateral surface may be strongly reticulate, bearing a number of short irregular thin ribs (*L.* (*L.*) *ostreata*) (Jones and Sherborn) or tuberculate and subspinose (*L.* (*L.*) *scabra bucki*). The marginal borders are smooth or feebly sculptured. Normal pore canals rather few, large and probably sieve-type. Marginal areas wide. Inner margin and line of concrescence coincide throughout. Selvage and flange generally well developed. Radial pore canals straight and well spaced ; 6–8 anteriorly, 3–4 posteriorly. Hinge entomodont and robust. Muscle scars consist of a vertical, oblique or crescentic line of four adductors, with one oval anterior and a smaller antero-ventral scar. Sexual dimorphism strongly pronounced, the male valves being longer and proportionally less high than the females. Instars, particularly the earlier growth stages, are more convergent posteriorly and have more angular cardinal angles than the adults.

Lophocythere (Lophocythere) scabra bucki Lutze 1960

Plate 8. Figs. 15–24. Plate 9. Figs. 1, 5.

1960 *Lophocythere scabra bucki* n. subsp. Lutze : 430, pl. 37, figs. 1–2.
1962 *Lophocythere scabra bucki* Lutze 1960. Brand and Fahrion : p. 148.

MATERIAL. 191, valves and carapaces.

DISTRIBUTION. Occuring in the *coronatum* zone of Staffin Bay ; and the *mariae* zone of Port-an-Righ and Staffin Bay. The species also occurs in England where it ranges from the *athleta* to the *cordatum* zone.

DIMENSIONS. From sample OC–Call–CH–14, *athleta* zone, Crook Hill, brickpit, Dorset.

		Length	Height	Width
Male R.V.	Io.5089	0·84	0·43	0·23
Male L.V.	Io.5090	0·84	0·45	0·23
Male Carapace	Io.5091	0·87	0·44	0·41
Female R.V.	Io.5092	0·70	0·40	0·24
Female L.V.	Io.5093	0·73	0·44	0·24
Female Carapace	Io.5094	0·72	0·44	0·39

ONTOGENY. A large number of the later growth stages occur at certain horizons ; some dimensions from sample OC–Call–CH–15, *athleta* zone of Crook Hill brickpit, Dorset, are given below :

	Length		Height		
	Range	Mean	Range	Mean	L.H. ratio
Adult					
All female 10 R.V, 10 L.V.	0·76–0·79	0·77	0·43–0·49	0·45	1·70 : 1
Penultimate Instar					
10 R.V., 10 L.V.	0·61–0·65	0·63	0·36–0·41	0·38	1·67 : 1
Antepenultimate Instar					
10 R.V., 10 L.V.	0·56–0·61	0·60	0·32–0·37	0·34	1·75 : 1
Antepenultimate Instar					
minus one. 10 R.V., 10 L.V.	0·44–0·47	0·46	0·26–0·29	0·27	1·71 : 1
Antepenultimate Instar					
minus two. 2 L.V.	0·33–0·36	0·35	0·21–0·23	0·22	1·61 : 1

These readings are too few to place any great reliance of them statistically, but they do raise a number of points of interest. The increase in the length : height ratio is not regular and two of the growth stage give higher readings than that of the adult stage and also, the mean height increase (0·05) is greater than the mean length increase (0·03). Amongst all the other species of Jurassic ostracods studies by the author, and mean length increase has always been greater than the mean height increment.

REMARKS. The present material is slightly larger than the type material from the Middle Callovian of N.W. Germany (Lutze 1960 L : 0·62–0·80 ; H. 0·32–0·42). The subspecies has been recorded once before from Britain, from the *mariae* zone of

Oxfordshire (Lutze 1960). This subspecies differs from *L.* (*L.*) *scabra scabra* Triebel 1951 in possessing a row of spatulate tubercules ventro-laterally instead of a rib.

Lophocythere (Lophocythere) interrupta interrupta Triebel 1951

Plate 9. Figs. 2–4, 6–10.

1949 Ostracod No. 886. Brand: 340, pl. 13, fauna 88, fig. 51.
1951 *Lophocythere interrupta* n. sp. Triebel : 96, pl. 47, figs. 35–41.
1960 *Lophocythere interrupta interrupta* Triebel 1951. Lutze : 431, pl. 36, fig. 6.
1962 *Lophocythere interrupta interrupta* Triebel 1951. Brand and Fahrion : 148, pl. 21, fig. 39.
1967 *Fastigatocythere interrupta interrupta* (Triebel 1951). Wienholz : 27, pl. 2, figs. 17–19.
1967 *Fastigatocythere interrupta directa* n. ssp. Wienholz : 28, pl. 2, figs. 20–22a ; pl. 3, figs. 22b–23.

MATERIAL. 145 valves and carapaces.

DISTRIBUTION. Confined to the Callovian: occurring in the *coronatum* zone at Brora. Also occurring in the *coronatum*, *athleta* and *lamberti* zones of Dorset.

DIMENSIONS. Sample OC–Call–Ba–77, *coronatum* zone, Brora.

		Length	Height	Width
Female L.V.	HU.19.J.41	0·87	0·49	0·28
Female L.V.	Io.5095	0·88	0·48	0·28
Female R.V.	HU.19.J.43	0·88	0·45	0·27
Male R.V.	HU.19.J.44	0·99	0·44	0·25
Male R.V.	Io.5096	1·00	0·45	0·28
Male Carapace	Io.5097	1·00	0·44	0·51
Female Carapace	Io.5098	0·87	0·48	0·49

ONTOGENY. The adult and the 5 preceeding growth stages occur ; some dimensions from sample OC–Call–T.Pt.–25, the *lamberti* of zone Tidmoor Point, are given below.

	Length		Height		
	Range	Mean	Range	Mean	L : H
Adult (Females) 8 R.V., 8 L.V.	0·81–0·85	0·81	0·41–0·47	0·44	1·86 : 1
Penultimate Instar 8. R.V., 8 L.V.	0·62–0·69	0·65	0·33–0·37	0·35	1·84 : 1
Antepenultimate Instar 8 R.V., 8 L.V.	0·48–0·52	0·50	0·27–0·30	0·28	1·80 : 1
Antepenultimate Instar minus one. 1 R.V., 4 L.V.	0·38–0·40	0·39	0·21–0·24	0·23	1·69 : 1
Antepenultimate Instar minus two. 4 L.V., 2 R.V.	0·31–0·32	0·31	0·18–0·20	0·17	0·64 : 1
Antepenultimate Instar minus three. 1 L.V.		0·26		0·17	0·56 : 1

Although there are insufficient measurements of the earlier growth stages to substantiate these results statistically, some interesting factors emerge. The length : height ratio exhibits a steady, but not regular increase from the earliest forms to the adult. Mean size increases are also irregular, as between the antepenultimate minus one and the antepenultimate stages and also between the penultimate and the adult.

Remarks. The present author does not agree with the action of the late Dr. Weinholz (1967) in placing this species in her new genus *Fastigatocythere*. As *L.* (*L.*) *interrupta interrupta* possesses an eye spot it is clearly disqualified from membership of *Fastigatocythere*. The species *interrupta* is thought to have been derived from the *L.* (*L.*) *scabra* stock by the gradual suppression of the strongly tuberculate ornament of the latter. The material described herein is considerably variable in ornament and although forms similar to those described by Weinholz (1967) as *Fastigatocythere interrupta directa* n. ssp. do occur, it has not been possible to consistently differentiate such forms as a discrete subspecies. They are, in consequence, included within the subspecies *interrupta interrupta*.

The subspecies occurs in the *jason*, *coronatum* and *athleta* zones of Germany. This is the first record of the subspecies in Britain and its range is extended by one zone, into the *lamberti*.

Subgenus ***NEUROCYTHERE*** n. subgen.

Type species. *Cythere bradiana* Jones 1884.

Derivato nominis. Greek. From the ' nerve ' like nature of the ribs.

Diagnosis. Subgenus of *Lophocythere* with usually 4 longitudinal ribs and reticulate intercostate areas. Ribs may or may not reach the anterior margin. Minor ribs lie between or connect the major ribs ; a small rib is associated with the eye tubercule.

Remarks. The majority of the species of this genus belong to *Neurocythere* which is particularly important in the Bathonian, Callovian and in the lower and middle parts of the Oxfordian where it often dominates the ostracod fauna. Its abundance, wide lateral distribution and diversity of relatively short-lived species render it of considerable importance as a zonal indicator and for general purposes of correlation.

Lophocythere (Neurocythere) cruciata alata n. subsp.

Plate 9. Figs. 11–16. Plate 10. Figs. 1–5, 8.

Diagnosis. Subspecies of *L.* (*N*) *cruciata* characterized by its strongly alate ventro-lateral rib, the discontinuous nature of the median rib and in having no ribs reaching the anterior margin.

Holotype. One left valve, HU.19.J.69, from sample OC–Call–SB–71, *lamberti* zone, Staffin Bay.

DERIVATO NOMINIS. Latin : from the alate nature of the vento-lateral rib.

MATERIAL. 436 valves and carapaces.

DISTRIBUTION. Restricted to the *lamberti* zone of Staffin Bay, Skye.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
L.V.	HU.19.J.69	0·73	0·49	0·28
PARATYPES	Same sample as holotype.			
L.V.	Io.5099	0·69	0·43	0·21
L.V.	Io.5100	0·73	0·49	0·27
R.V.	Io.5101	0·72	0·43	0·27
R.V.	Io.5102	0·75	0·43	0·28
R.V.	Io.5103	0·69	0·43	0·21
Carapace	Io.5104	0·71	0·44	0·39
Carapace	HU.19.J.76	0·68	0·41	0·40

DESCRIPTION. Medium to large. Subrectangular to subquadrate, inflated ventrally. Left valve larger than right with strong dorsal overlap. Anterior margin broadly rounded ; posterior caudate with apex above mid-height, more dorsal and more pointed in right than in left valves. Dorsal margin straight, ventral margin medianly concave. Greatest length above mid-height ; height and width in the posterior third of the valve. Surface ornament of longitudinal ribs with intercostal reticulations which are coarsest on the flanks of the ribs, particularly the ventral and ventro-lateral. The ventral rib extends in a shallow curve from the ventral part of the caudal process to an antero-ventral position. The ventro-lateral rib, which medianly becomes strongly alate, extends from a postero-ventral position to its antero-median junction with the anterior part of the median rib. The median rib is somewhat tenuous and is often interrupted medianly by a sulcus. The dorsal rib is variable. In the right valve it extends from a postero-dorsal position in an arc to its termination, just behind the eye spot. In the left valve it fringes the dorsal margin, passing dorsal to the eye spot, and is terminated on the anterior marginal border. A short rib extends from the eye spot to the junction of the median and ventro-lateral ribs. Three narrow ribs occur on the ventral surface. No ribs reach the anterior margin. Eye spot circular, glassy and prominent. Marginal areas wide, particularly anteriorly ; inner margin and line of concrescence coincident throughout. Radial pore canals straight, well-spaced ; 8 anteriorly and 2 posteriorly. Hinge entomodont, well developed. The terminal elements in the right valve are raised dentate ridges, each with 6 teeth. The median element is variable ; in some forms it is a locellate groove, narrowing and shallowing but little posteriorly ; in others the posterior part is a shallow locellate groove and in yet others the groove widens and deepens in the posterior 1/4 of its extent. Complementary structures occur in the left valve hinge, above which is a long, gutter-like accommodation groove. Muscle scars of 4 vertical adductors with a large anterior and a much smaller antero-ventral scar.

ONTOGENY. The adult and the three preceeding growth stages are recorded.

Some dimensions from sample OC–Call–SB–70 are given below : In all stages except the youngest, (2 R.V., 2 L.V.) 10 R.V. and 10 L.V. are measured.

	Length		Height		
	Range	Mean	Range	Mean	L : H
Adult	0·65–0·71	0·66	0·30–0·45	0·38	1·77 : 1
Penultimate Instar	0·59–0·61	0·60	0·32–0·39	0·35	1·72 : 1
Antepenultimate Instar	0·52–0·55	0·53	0·31–0·32	0·31	1·71 : 1
Antepenultimate Instar minus one.	0·44–0·47	0·46	0·26–0·29	0·28	1·65 : 1

The adults of this species are very variable in size as can be seen from the above dimensions and from those of the paratypes. A gradual increase in the length : height ratio can be seen from the youngest form to the adult. Overlap may occur in the height of the various growth stages, but not in the length.

REMARKS. *L.* (*N.*) *cruciata alata* differs from all other subspecies of *cruciata* in the possession of a very strong alate ventro-lateral rib. Its origins are obscure and its true relationships difficult to assess, due to its isolation and restriction to the Hebrides. It appears to be most closely related to *L.* (*N.*) *cruciata intermedia* from which it could have been derived by the increasingly alate development of the ventro-lateral rib.

Lophocythere (Neurocythere) cruciata intermedia Lutze 1960

Plate 10. Figs. 6, 7, 9–21. Plate 11, Figs. 1, 4.

1960 *Lophocythere cruciata intermedia* n. subsp. Lutz : 423, figs. 5–6.

MATERIAL. 288 valves and carapaces.

DISTRIBUTION. Occurring at all three localities in Scotland ; in the *coronatum* zone of Brora ; the *lamberti* and *mariae* zones of Staffin Bay ; and the *mariae* zone of Port-an-Righ. In England it occurs at a number of localities and ranges from the *athleta* to the *cordatum* zone.

DIMENSIONS. Sample OC–Call–T.Pt.–26, *lamberti* zone, Tidmoor Point, Dorset.

		Length	Height	Width
Female R.V.	Io.5106	0·59	0·35	0·17
Female L.V.	Io.5107	0·58	0·37	0·19
Male R.V.	Io.5108	0·64	0·35	0·19
Male R.V.	HU.19.J.80	0·61	0·35	0·19
Female Carapace	Io.5109	0·59	0·36	0·35
Male Carapace	Io.5110	0·64	0·36	0·34

ONTOGENY. The adult and the two preceeding growth stages occur. 10 RV and 10 LV from each growth stage are measured, from sample OC–Call–CH–19, *athleta* zone, Crook Hill brickpit, Dorset.

	Length		Height		
	Range	Mean	Range	Mean	L : H
Adult	0·49–0·52	0·51	0·28–0·32	0·30	1·69 : 1
Penultimate Instar	0·43–0·45	0·44	0·23–0·25	0·24	1·81 : 1
Antepenultimate Instar	0·35–0·40	0·37	0·19–0·23	0·21	1·79 : 1

REMARKS. This subspecies has been recorded twice before from Britain, by Lutze (1960) from the *athleta* zone of Crook Hill, and from the *lamberti* zone of Woodham. The present records from the *mariae* and *cordatum* zones are an extension of the known range by two zones, and the first record from the Oxfordian. The subspecies is thought to be ancestral to *L.* (*N.*) *cruciata oxfordiana* Lutze, from which it is distinguished by its more quadrate outline, and in its possession of vertical ribs connecting the dorsal and median ribs. It differs from *L.* (*N.*) *cruciata alata* n. subsp. in lacking a strongly alate ventro-lateral rib.

Lophocythere (Neurocythere) cruciata oxfordiana Lutze 1960

Plate 11. Figs. 2, 3, 5–17.

1958 *Lophocythere cruciata cruciata* Triebel 1951. Bizon : 24, pl. 3, fig. 9.
1959 *Lophocythere cruciata cruciata* Triebel 1951. Oertli : 32–33, pl. 4, figs. 128–132.
1960 *Lophocythere cruciata oxfordiana* n. subsp. Lutze : 425–426, pl. 33, fig. 5.
1962 *Lophocythere cruciata oxfordiana* Lutze 1960. Brand and Fahrion : 147, pl. 21, fig. 43.
1962 *Lophocythere cruciata oxfordiana* Lutze 1960. Klingler, Malz and Martin : 184, pl. 25, fig. 2.
1963 *Lophocythere cruciata oxfordiana* Lutze 1960. Oertli, pl. XXXVII, 2.

MATERIAL. 1268 valves and carapaces.

DISTRIBUTION. This subspecies is widespread throughout the lower and middle part of the Oxfordian in Britain, ranging from the base of the *mariae* to the middle of the *cautisnigrae* zone. In Scotland it occurs in the *mariae* and *cordatum* zones at Staffin Bay ; and the *mariae* zone of Port-an-Righ.

DIMENSIONS. OC–Ox–Pn–25, *cordatum* zone Purton, Wilts.

		Length	Height	Width
Female R.V.	Io.5111	0·53	0·32	0·17
Female L.V.	Io.5112	0·55	0·36	0·19
Male R.V.	Io.5113	0·64	0·31	0·18
Male L.V.	HU.19.J.86	0·64	0·36	0·19
Female Carapace	Io.5114	0·55	0·35	0·29
Male Carapace	Io.5115	0·61	0·35	0·30

ONTOGENY. The adult and the four preceeding growth stages are recognised. Dimensions from sample OC–Ox–Pn–25, *cordatum* zone, Purton, Wilts. are given below. For each stage except the earliest (3 R.V., 3 L.V.), 10 R. and 10 L. valves are measured. In the adult stage, half of the specimens belong to each sex.

		Length		Height	
	Range	Mean	Range	Mean	L : H
Adult	0·52–0·64	0·58	0·31–0·36	0·34	1·73 : 1
Penultimate Instar	0·48–0·41	0·50	0·27–0·29	0·28	1·76 : 1
Antepenultimate Instar	0·43–0·49	0·46	0·25–0·26	0·26	1·80 : 1
Antepenultimate Instar minus one.	0·37–0·41	0·39	0·21–0·24	0·23	1·73 : 1
Antepenultimate Instar minus two.	0·30–0·32	0·31	0·17–0·20	0·17	1·85 : 1

Remarks. The subspecies varies greatly in size and shape both geographically and chronologically. Previous records have not mentioned sexual dimorphism which is, amongst the present material, pronounced at certain horizons, particularly in the *mariae* zone. The earlier forms are more quadrate than those occuring at higher levels and show a closer affinity to *L.* (*N.*) *cruciata intermedia* Lutze, from which *oxfordiana* is thought to have been derived. *L.* (*N.*) *oertlii* Bizon is similar, but in the latter, the ' cruciform ' arrangement of the ribs is lost because the rib from the eye spot extends to the anterior margin instead of to the junction of the median and ventro-lateral ribs. Glashoff (1964) regards this subspecies as being synonymous with *L.* (*N.*) *oertlii* and discusses an ' *oxfordians* ' type of the latter species. Amongst the present material, however, the two species are quite distinctive and the present author cannot find any evidence to justify their being considered conspecific. Lutze (1960) describes this species as ranging down into the *lamberti* zone in N.W. Germany. The present material exhibits a somewhat greater range in length (0·53–0·64) than the type material (0·54—0·60).

Lophocythere (Neurocythere) cruciata cruciata Triebel 1951

Plate 11. Figs. 18–22.

1949 Ostracode No. 896. Brand : 338, pl. 13, fauna 7, fig. 5, pl. 14.
1951 *Lophocythere cruciata cruciata* n. subsp. Triebel : 99, 100, pl. 49, figs. 53–56.
1962 *Lophocythere cruciata cruciata* Triebel 1951. Brand and Fahrion : 146, pl. 21, fig. 29.
1967 *Lophocythere cruciata cruciata* Triebel 1951. Weinholz : pl. 5, figs. 62–63.
non 1958 *Lophocythere cruciata cruciata* Triebel 1951. Bizon : 24, pl. III, fig. 10.
non 1959 *Lophocythere cruciata cruciata* Triebel 1951. Oertli : 32, pl. 14, figs. 128–132.

Material. 9 valves and carapaces.

Distribution. Occuring in Britain only in the *coronatum* zone of Brora.

Dimensions. Sample OC–Call–Ba–77, *coronatum* zone, Brora.

		Length	Height	Width
Female L.V.	Io.5116	0·73	0·44	0·27
Female Carapace	Io.5117	0·79	0·47	0·43

Remarks. This is the first record of the subspecies from Britain. The ribs of the present specimens are less well developed than the type material and the reticulations proportionally stronger.

Lophocythere (Neurocythere) flexicosta lutzei n. subsp.

Plate 12. Figs. 1–12.

1960 *Lophocythere flexicosta* n. subsp. A. Lutze : 428–429, pl. 36, figs. 2–3.
1962 *Lophocythere flexicosta* subsp. A. Lutze 1960. Brand and Fehrion : 149, pl. 21, fig. 41.
1963 *Lophocythere flexicosta* subsp. A. Lutze 1960. Oertli, pl. XXXIV, 1, 2, XXXV, 1.
1967 *Lophocythere flexicosta* ssp. A. Lutze 1960. Wienholz : pl. 5, fig. 57.

DIAGNOSIS. A strongly dimorphic subspecies of *flexicosta*, characterized by its rectangular outline and smooth, thick ribs. The dorsal and median ribs are always united posteriorly, the reticulations on the flanks of the ribs are very coarse.

HOLOTYPE. One female right valve, HU.19.J.102. From sample OC–Call–Wm–24, *athleta* zone Woodham brickpit.

DERIVATO NOMINIS. In honour of Dr. G. F. Lutze who first recognized the subspecies, in recognition of his valuable contributions to our understanding and appreciation of Jurassic microfossils.

MATERIAL. 300 valves and carapaces.

DISTRIBUTION. In Scotland occuring only in the *coronatum* zone at Brora. In England it ranges from the *athleta* to the *lamberti* zone.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
Female R.V.	HU.19.J.102	0·63	0·36	0·16
PARATYPES	Same sample as holotype.			
Female R.V.	Io.5118	0·73	0·40	0·19
Male R.V.	Io.5119	0·87	0·40	0·17
Male L.V.	Io.5120	0·89	0·44	0·17
Male Carapace	Io.5121	0·89	0·43	0·36
Female Carapace	Io.5122	0·71	0·43	0·33

DESCRIPTION. Medium to large. Thick shelled. Subrectangular, strongly dimorphic. Left valve larger than right with conspicuous dorsal overlap. Anterior margin rounded ; posterior bluntly pointed. Dorsal margin straight ; ventral with slight median concavity ; both margins largely obscured in lateral view by the overhang of the dorsal and ventral ribs respectively. Greatest length at mid-height ; height, at the anterior cardinal angle ; width, medianly. Sculpture of broad smooth ribs and intercostate reticulations which are particularly coarse on the flanks of the ribs. A complex of ramifying and anastomosing ribs occurs antero-medianly. The ventral rib extends in a shallow curve from the ventral part of the posterior margin to this complex. The ventro-lateral rib which extends from a mid-posterior position, and the median rib which extends from a postero-dorsal position, both lose their identity in the antero-median complex. The dorsal rib, which is united posteriorly to the median rib, extends in an arc across the dorso-lateral surface to this complex and a short rib extends ventrally from the eye spot also to this complex. A number

of narrow ribs occur on the ventral surface and may extend on to the antero-marginal border. The eye spot is large and prominent. The valve surface slopes steeply from the anterior margin to the lateral surface. Marginal areas wide ; line of concrescence and inner margin coincide throughout. Selvage well developed, and a frill-like flange occurs both anteriorly and posteriorly. Radial pore canals straight and well-spaced ; 6–8 anteriorly, 2–4 posteriorly. Hinge entomodont and very strongly developed, with proportionally long terminal elements. In the right valve, the anterior terminal element is an elongate dentate ridge with 5 oval, sometimes bifid teeth. The posterior terminal element has 7 teeth, which apart from the posterior two, decrease in size and height proximally. The median element comprises a deep loculate groove with 5 locules anteriorly and a shorter locellate groove posteriorly. The median element is bounded ventrally by a strong ridge, which expands distally to form the terminal elements. Complementary structures occur in the left valve hinge, above which is a narrow, shelf-like accommodation groove. Muscle scars consist of four vertically disposed adductors with a large anterior and a much smaller antero-ventral scar. Sexual dimorphism strongly pronounced, the male valves being longer and proportionally less high than the females.

Ontogeny. The adult and the three preceeding growth stages occur. Dimensions from sample OC–Call–CH–14, *athleta* zone, Crook Hill, are given below. In this population, all the adults are females. 10 R.V. and 10 L.V. are measured for each stage.

	Length		Height		
	Range	Mean	Range	Mean	L : H
Adult	0·69–0·73	0·71	0·38–0·43	0·40	1·73 : 1
Penultimate Instar	0·56–0·58	0·57	0·29–0·33	0·32	1·80 : 1
Antepenultimate Instar	0·42–0·45	0·44	0·24–0·26	0·25	1·82 : 1
Antepenultimate Instar minus one.	0·33–0·35	0·34	0·20–0·21	0·20	1·09 : 1

The length : height ratio shows a sharp increase from the earliest growth stage to the antepenultimate, followed by a slight decrease to the adult. Although the earlier forms have merodont hingement and weak ribs, the penultimate instar has the same hinge and sculpture as the adult.

Remarks. This subspecies has been previously recorded from Britain as *L. flexicosta n. subsp. A.* from the *athleta* zone of Woodham brickpit by Lutze 1960. This subspecies differs from *L.* (*N.*) *flexicosta flexicosta* Triebel in its larger size and more rectangular shape and in its stronger and smoother ribs.

The present material is somewhat larger than that described from N.W. Germany, (Lutze 1960).

	Length	Height
N.W. Germany	0·67–0·85	0·37–0·44
Britain	0·68–0·89	0·36–0·46

Genus ***FUHRBERGIELLA*** Brand and Malz 1962

Subgenus ***PRAEFUHRBERGIELLA*** Brand and Malz 1962

REMARKS. This subgenus differs on grounds of ornament from its closest allies. *Glyptocythere, Progonocythere, Lophocythere* s.l. It may be ancestral to *Lophocythere,* The species *F.* (*P.*) *horrida* Brand and Malz, described below, has not previously been recorded from above the Bajocian, and this present record is an extension of the known range of the genus up into the lower Oxfordian.

Fuhrbergiella (Praefuhrbergiella) horrida horrida Brand and Malz 1962

Plate 12. Figs. 13–15., Plate 13. Figs. 1–5.

1960 Ostracode No. 10. Lutze : 435, pl. 38, fig. 5.
1962 *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* n. subsp. Brand and Malz : 19–21, pl. 4, figs. 33–37, pl. 5, fig. 46.
1962 *Fuhrbergiella* (*Praefuhrbergiella*) *horrida horrida* Brand and Malz 1962. Brand and Fahrion : 141, pl. 20, fig. 52.

MATERIAL. 41, valves and carapaces.

DISTRIBUTION. In Scotland occuring in the *mariae* zone at Port-an-Righ and ranging from the *lamberti* to the *cordatum* zone at Staffin Bay. Also recorded from the *koenigi* and *cordatum* zones in England.

DIMENSIONS. Sample Kell-Pl–2 Kellaways Clay, Putton Lane brickpit, Nr. Weymouth, Dorset. *koenigi* zone.

		Length	Height	Width
Female Carapace	Io.5123	0·62	0·35	0·19
Sample OC–Ox–Pn–31, *cordatum* zone, Purton, Wilts.				
Male R.V.	Io.5124	0·68	0·36	0·33

ONTOGENY. The adult and the 4 preceeding growth stages occur. Some dimensions from sample OC–Ox–Pn–31, *cordatum* zone Purton, Wilts, are given below:

	Length	Height
Adult R.V.	0·67	0·36
Penultimate Instar L.V.	0·56	0·35
Antepenultimate Instar L.V.	0·41	0·27
Antepenultimate Instar minus one L.V.	0·35	0·21
Antepenultimate Instar minus two L.V.	0·27	0·19

REMARKS. This species is extremely variable with the surface ornament either coarsely reticulate or irregularly spinose. A similar variation is to be seen in the illustrations of the type material.

Family **PROTOCYTHERIDAE** Lyubimova 1955

REMARKS. In the American Treatise (1961, Q327) the subfamily Protocytherinae Lyubimova 1955, is considered as a subfamily of the Progonocytheridae Sylvester-

Bradley 1948. Bate (1963a, p. 209) removed this subfamily from the Progonocytheridae and elevated it to the status of family. The present author would also include here the Pleurocytherinae Mandelstam 1960, rather than retain it in the Progonocytheridae as done by Bate (1963).

Subfamily **PLEUROCYTHERINAE** Mandelstam 1960

Genus ***PALAEOCYTHERIDEA*** Mandelstam 1947

REMARKS. This genus was erected by Mandelstam with *Palaeocytheridea bakirovi* Mandelstam as type species. Contrary to the rules of the I.C.Z.N., Lyubimova (1955) and later Mandelstam (1960) decided that *P. bakirovi* was not a typical member of the genus and designated a different type species. This second type, *Eucythere denticulata* Sharapova 1937, is very different from *P. bakirovi* and cannot be included within the genus *Palaeocytheridea* as originally defined. Therefore, the genus *Palaeocytheridea* sensu Lyubimova 1955 and Mandelstam 1960 is invalid and must be suppressed. *Palaeocytheridea* (sensu Mandelstam 1947) is placed here tentatively in the Pleurocytherinae because of its close similarity to *Pleurocythere*.

Palaeocytheridea parabakirovi Malz 1962

Plate 13. Figs. 6–9.

1962 *Palaeocytheridea parabakirovi* n. sp. Malz : 236–239, pl. 24, figs. 2–4.
1967 *Palaeocytheridea parabakirovi* Malz, 1962. Wienholz : pl. 5, figs. 65–66.

MATERIAL. 18 valves and carapaces, mostly fragmentary.

DISTRIBUTION. Occurring in the *coronatum* zone at Brora, and the *macrocephalus* zone of Dorset.

DIMENSIONS. Sample OC–Call–Ba–87, *coronatum* zone Brora.

		Length	Height	Width
Carapace	Io.5125	0·60	0·35	0·28

REMARKS. The present material is very similar in size to the type, from the *jason* zone of N.W. Germany. This species differs from *P. bakirovi* Mandelstam in possessing a dorsal rib extending ventrally from the anterior cardinal angle and in lacking a rib between the median and ventro-lateral ribs. This is the first record of the species in Britain.

Genus ***PLEUROCYTHERE*** Triebel 1951

REMARKS. *Pleurocythere* is very similar to *Protocythere* Triebel, particularly with regard to the nature of the radial pore canals and hingement. *Protocythere* has only 3 ribs, which are usually much more swollen than those of *Pleurocythere*, and also has a very marked anterior hinge ear in the left valve. *Pleurocythere* would appear to be ancestral to *Protocythere*, and the species of the former here described show much

closer affinities to such Jurassic species of *Protocythere* as *P. sigmoidea* Steghaus and *P. rodewaldensis* (Klingler), than to the better known Lower Cretaceous forms. The species of *Pleurocythere* here described are the first recorded from the British Callovian and Oxfordian, where they form a not unimportant element of the ostracod fauna. A striking, but superficial similarity to some of the contemporary species of *Lophocythere* (*Neurocythere*) is observed. In N.W. Germany, of the large fauna of *Pleurocythere* species described by Triebel (1951), none extended above the Bathonian. The present record of the genus extending up into the *cordatum* zone in Britain, is a considerable extension of the known range of the genus. *Protocythere quadricarinata* Swain and Peterson 1952, from the equivalent of the mariae zone of North America, is probably better accommodated in *Pleurocythere*. The present author does not accept Wienholz' (1967) subdivision of the genus into *Pleurocythere* s.s. and the new subgenus *Sabacythere*. The reasons given for these subdivisions are not more than is consistent with variation within a genus.

Pleurocythere borealis borealis sp. nov. subsp. nov.

Plate 13. Figs. 10–24.

DIAGNOSIS. Elongate *Pleurocythere* with well rounded anterior and bluntly pointed posterior margins. Sculpture of very weak longitudinal ribs and smooth or minutely punctate intercostate areas.

HOLOTYPE. One male right valve, HU.20.J.22 sample OC–Ox–SB–77, mariae zone Staffin Bay.

DERIVATO NOMINIS. From its apparent restriction to the Jurassic of N.W. Scotland.

MATERIAL. 23 valves and carapaces.

DISTRIBUTION. Occurring in a single sample from the *mariae* zone of Staffin Bay, Skye.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
Male R.V.	HU.20.J.22	0·68	0·33	0·16
PARATYPES				
Male R.V.	Io.5126	0·72	0·33	0·17
Female R.V.	Io.5127	0·64	0·33	0·17
Male L.V.	Io.5128	0·70	0·37	0·17
Female L.V.	Io.5129	0·68	0·37	0·17
Female Carapace	Io.5130	0·68	0·40	0·31

DESCRIPTION. Medium to large, subrectangular, elongate, Dimorphic, males longer and less high than females. Left valve larger than right with considerable dorsal overlap. Anterior margin asymmetrically rounded with extremity below mid-height. Posterior margin bluntly pointed, apex at mid-height. Dorsal and ventral margins with slight median concavities. Greatest length below mid-height ;

height, at the anterior cardinal angle ; width, postero-ventrally. Sculpture of longitudinal ribs, with smooth or minutely punctate intercostate areas. There are three major ribs. The ventro-lateral rib extends from a postero-ventral position to its tenuous junction with the median rib antero-medianly. The median rib extends diagonally across the valve from a postero-median position to this junction. The dorsal rib is very weak, particularly in the left valve. The inverted ' Y '-shaped rib associated with the eye tubercule, which is characteristic of the genus, is poorly developed. Small longitudinal, vertical and oblique ribs occur between the major ribs. One or more small tubercules occur posteriorly. Eye spot weakly developed. Normal pore canals few and scattered. Marginal areas wide antero-ventrally, of medium width elsewhere. Inner margin and line of concrescence coincident throughout. Selvage strong ventrally. Radial pore canals long and thin, slightly sinuous and slightly thickened at their extreme distal extent ; 9 anteriorly, concentrated antero-ventrally with the most dorsal slightly upturned ; 5 posteriorly, the most dorsal two being vertically inclined. A variable number of false canals occur anteriorly. Hinge antimerodont. In the right valve, the terminal elements are raised dentate ridges each with 6 teeth, which are weakly incised dorsally. The median element is a long locellate groove, open ventrally and bounded dorsally, by a smooth bar. Complementary structures occur in the left valve hinge, where the terminal elements are open ventrally and distally. Accommodation groove shallow and gutter-like.

Remarks. This subspecies differs from *Pleurocythere borealis carinata* n. subsp. in its more rounded cardinal angles and less well developed major ribs. From the type species, *P. richteri* Triebel 1951, it differs in possessing weaker and much thinner ribs, although the outline of the two is very similar. *Pleurocythere* (*Sabacythere*) *arcuata* Wienholz (1967) is very similar but considerably shorter with a range in length of 0·59–0·62 for females and 0·63–0·66 for males, compared with 0·64–0·68 for females and 0·68–0·72 for males in the present material. As the two subspecies of *P. borealis* described herein are recorded from the *mariae* and *cordatum* zones of the Oxfordian, it seems almost certain that *P. arcuata* from the *lamberti* zone of Germany, is an ancestral form.

Pleurocythere borealis carinata n. subsp.

Plate 14. Figs. 1–12, 14.

Diagnosis. Subspecies of *Pleurocythere borealis* with thin but well defined longitudinal ribs. A prominent rib lies between the median and ventro-lateral ribs.

Holotype. One female left valve, HU.20.J.28, sample OC–Ox–SB–83, *mariae* zone Staffin Bay, Skye.

Derivato nominis. Because of the relatively strong ribbing developed in this subspecies.

Material. 18, valves and carapaces.

DISTRIBUTION. From the *coronatum* zone at Brora, and the *mariae* zone at Staffin Bay.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
Female L.V.	HU.20.J.28	0·61	0·37	0·17
PARATYPES	Same sample as Holotype.			
Male L.V.	Io.5131	0·63	0·31	0·15
Male R.V.	Io.5132	0·64	0·33	0·16
Female Carapace	Io.5133	0·63	0·38	0·32

DESCRIPTION. Medium ; subrectangular. Dimorphic ; males slightly longer and less high than females. Left valve larger than right with dorsal overlap. Anterior margin well-rounded in left valve, rather more angular in right ; extremity below mid-height. Posterior margin more pointed in right than left valve ; apex at mid-height. Dorsal margin straight, overhung in right valve by dorsal rib. Ventral margin with slight median concavity, medianly obscurred by valve tumidity. These margins converge posteriorly, particularly in right valves. Greatest height at the anterior cardinal angle ; width, postero-ventrally. Sculpture of longitudinal ribs with smooth or finely punctate intercostate areas. There are three major ribs. The ventro-lateral rib extends across the valve to its antero-median junction with the median rib, the latter extending to this junction from a postero-median position. In the right valve the median rib is continuous, in the left it is interrupted medially. The dorsal rib extends from a postero-dorsal position, in an arc across the dorsal-lateral surface to its termination posterior to the eye tubercule. This rib is most strongly developed in the right valve where it overhangs the dorsal margin. A short rib occupies the posterior part of the area between the ventro-lateral and the median ribs, and another in the form of an inverted ' Y ', extends vertically from the eye spot. A number of weak ribs occur on the ventral surface. A short rib may connect the ventro-lateral and median ribs anteriorly. Eye tubercule small. Normal pores most numerous ventrally. Marginal areas widest anteriorly. Inner margin and line of concrescence coincide throughout. Nine radial pore canals, with slight distal thickenings occur anteriorly together with 3 false canals. These canals are concentrated antero-ventrally and the most dorsal are upturned. 5 canals occur posteriorly, of which the two most dorsal are vertically inclined. Hinge antimerodont and strongly developed. The terminal elements in the right valve are strong elongate dentate ridges with 6 teeth anteriorly and 7 posteriorly. These teeth are secondarily incised dorsally and increase in height distally. The median element is a locellate groove, ventrally closed at its extremities but open medially. The distal ventral wall of this groove are expanded distally to form the terminal elements. Complementary structures occur in the left valve hinge, where the loculate terminal elements are open distally. The accommodation groove is wide and shelf-like. There are four vertically aligned adductors and a single heart-shaped anterior scar.

REMARKS. The differences between this subspecies and *P. borealis borealis* n.

subsp. are outlined in the ' Remarks ' of the latter. From *P. richteri* Triebel *P. borealis carinata*, differs in its thinner ribs, in possessing a rib between the median and ventro-lateral ribs, and in its more angular anterior cardinal angle.

Pleurocythere caledonia n. sp.

Plate 14. Figs. 13, 15–24. Plate 15. Figs. 1–4, 11.

DIAGNOSIS. A new species of the genus *Pleurocythere* characterised by its strongly assymmetrical anterior margin and antero-ventral marginal spines.

HOLOTYPE. One female left valve HU.20.J.32, sample OC–Call–SB–71, *lamberti* zone, Staffin Bay, Skye.

DERIVATO NOMINIS. From its apparent restriction to the Jurassic of Scotland.

MATERIAL. 155 valves and carapaces.

DISTRIBUTION. Ranging from the *lamberti* to the *cordatum* zone at Staffin Bay, and from the *mariae* to the *cordatum* zone at Port-an-Righ.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
Female L.V.	HU.20.J.32	0·68	0·39	0·18
PARATYPES	From the same sample as the Holotype.			
Female L.V.	Io.5134	0·69	0·40	0·19
Male L.V.	Io.5135	0·69	0·36	0·18
Male L.V.	Io.5136	0·69	0·36	0·19
Male R.V.	Io.5137	0·71	0·36	0·21
Female R.V.	Io.5138	0·64	0·35	0·22
Female Carapace	Io.5139	0·68	0·40	0·33

DESCRIPTION. Medium ; subrectangular, elongate. Dimorphic ; males slightly longer and proportionally less high than the females, the latter also being less convergent posteriorly. Left valve larger than right with considerable dorsal overlap. Anterior margin subangular with ventral extremity accentuated by a variable number (up to 18) of antero-ventral margins spines which are usually upturned. Posterior margin caudate, with apex at or near mid-height and more pointed in male than female valves. Marginal denticles may also occur postero-ventrally. Dorsal margin straight or medianly concave ; a poorly developed hinge-ear is present anteriorly in the left valve. Ventral margin medianly concave. These margins converge more strongly in right than in left valves. Greatest height at the anterior cardinal angle, 1/5th of the distance from the anterior margin ; greatest width postero-ventrally. Surface sculpture of longitudinal ribs, small circular tubercules and intercostate reticulations which are strongest on the flanks of the ribs. The ribs are usually more strongly developed in the right than in the left valve. On the ventral and ventro-lateral surfaces, some 6 or 7 small ribs occur. Some of these ribs extend from a postero-ventral to a ventro-median position ; others from a ventro-median to an antero-median position. None extend the entire length of the valve.

One of these ribs is upturned anteriorly to join the median rib. There is a small circular tubercule immediately anterior to this junction. The median rib extends from a posterodorsal to an antero-median position and may be broken medianly. In right valves, the dorsal rib extends from its postero-dorsal junction with the median rib, in an arc across the dorsal surface of the valve to its termination posterior to the posterior branch of the eye tubercule rib. It overhangs the dorsal margin and is often interrupted mid-dorsally. In the left valve, the rib is much weaker and does not overhang the margin. A short, but prominent eye tubercule rib extends in the form of an inverted 'Y' ventrally from the anterior cardinal angle ; another lies between the median and ventro-lateral ribs and a further short rib connects the median and ventro-lateral ribs anteriorly. Several smooth circular tubercules occur posteriorly ; one at the posterior cardinal angle, one at the junction of the dorsal and median ribs, and one or two postero-ventrally. Eye spot largely obscured by its associated rib. Marginal areas wide anteriorly. Inner margin and line of concresence coincide throughout. Selvage strongly developed ventrally. Radial pore canals thin, slightly sinuous and thickened distally ; 8–10 anteriorly with some false canals ; 4–6 posteriorly, the most dorsal of which is vertically inclined. Hinge antimerodont. In the right valve, the terminal elements are long dentate ridges with 5–6 smooth teeth anteriorly and 6–7 rather larger teeth posteriorly. All these teeth exhibit a faint secondary dorsal crenulation. The median element is a long locellate groove, open ventrally. The left valve hinge contains complementary structures and the terminal loculate sockets are open ventrally and distally. The accommodation groove is shelf-like with a central shallow, gutter-like groove. Muscle scars consist of a crescentric line of 4 adductors with a single heart-shaped anterior scar.

Remarks. This species differs from all other known species of *Pleurocythere* in the shape and spinose nature of the anterior margin. It is probably most closely related to such Bathonian species as *P. connexa* and *P. favosa* Triebel 1951, but differs in significant details of shape and ornament. Some variation is apparent throughout the observed range of the species ; for example, the *lamberti* zone forms are rather more elongate and have stronger marginal denticulations than do those from higher horizons.

Subfamily **KIRTONELLINAE** Bate 1963

Genus ***PSEUDOHUTSONIA*** Wienholz 1967

Remarks. The present author would place this genus, together with *Hutsonia* and *Loonyella*, in the *Kirtonellinae* Bate, on grounds of shape, ornament, hingement and musculature. *Balowella*, Wienholz (1967) is in the present author's opinion, congeneric with *Pseudohutsonia*.

Pseudohutsonia hebridica n. sp.

Plate 15. Figs. 5–10, 12–14, 16, 18.

Diagnosis. Species of *Pseudohutsonia* characterised by a strong ventro-lateral rib ; a series of narrow ribs radiating from the dorsal margin and a small but prominent median tubercule.

HOLOTYPE. One female L.V. HU.20.J.66, sample OC–Ox–SB–77, *mariae* zone, Staffin Bay, Skye.

DERIVATO NOMINIS. From its apparent restriction to the Jurassic of the Hebrides.

DISTRIBUTION. Occurring only at Staffin Bay, and ranging from the *lamberti* to the *cordatum* zone.

MATERIAL. 137 valves and carapaces.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
Female L.V.	HU.20.J.66	0·53	0·32	0·17
PARATYPES	From the same sample as the holotype.			
Female L.V.	Io.5140	0·53	0·32	0·17
Female R.V.	Io.5141	0·53	0·30	0·15
Female R.V.	Io.5142	0·56	0·30	0·16
Female Carapace	Io.5143	0·53	0·33	0·27

DESCRIPTION. Medium, subrectangular to sub-ovate. Dimorphic ; two broken but distinctly more elongate valves occurring and presumed to be males. Anterior margin rounded, extremity at, or below mid-height ; posterior margin caudate with apex above mid-height. Dorsal margin straight in right valve ; medianly concave in left, with weak anterior hinge ear. Ventral margin upturned posteriorly, largely obscured in lateral view by valve tumidity. Greatest height in anterior third ; width, ventro-medially. Left valve larger than right with dorsal overlap; left valve also deeper than right. The main feature of the surface sculpture is a strong smooth rib extending ventrally from the anterior cardinal angle and then curving posteriorly to extend in an arc across the ventro-lateral surface. Radiating from the dorsal margin, and extending towards this rib, are a series of 4 or 5 narrow ribs. A slight median sulcus occurs, anterior to which is a well defined tubercule. The anterior and posterior marginal borders are smooth. Three to 5 thin ribs lie between the main rib and the ventral margin. Intercostate areas are smooth. Eye spot absent. Normal pore canals moderately numerous, concentrated ventrally. Marginal areas rather narrow ; widest postero-ventrally. A slight anterior vestibule may occur ; inner margin and line of concrescence usually coincident throughout. Radial pore canals short and straight ; 8 anteriorly, 3 posteriorly. A thin frill-like flange occurs anteriorly. Hinge antimerodont. In the right valve the terminal elements are rather low dentate ridges with 5 teeth anteriorly and 7 posteriorly. The median element is a locellate groove which is ventrally closed distally and bounded dorsally by a smooth bar. The distal ventral bounding ridge of the median element is expanded distally to form the terminal elements. Complementary structures occur in the left valve hinge, above which is a gutter-like accommodation groove. Muscle scars consist of a vertical line of 4 adductors and two widely spaced anterior scars of which the dorsal is the larger.

REMARKS. This species would appear to be most closely allied to *Protocythere attendens* Lyubimova 1955, which is best accommodated in *Pseudohutsonia* but differs

in possessing a more prominent sculpture of thinner and better defined ribs. From *P. tuberosa* Wienholz it differs in lacking broad swellings dorso-laterally. Very little variation occurs throughout the range of the species although the younger members are somewhat thicker shelled and have more subdued sculpture than the earlier forms.

Pseudohutsonia sp. A.

Plate 15. Figs. 15, 20, 21.

1958 *Hutsonia* (?) sp. Bizon : 29, pl. 3, figs. 12–14, pl. 4, figs. 17–18.
1964 *Hutsonia* sp. Glashoff : 46, not figured.

MATERIAL. One male L.V., one female carapace.

DISTRIBUTION. From the *cordatum* zone of Port-an-Righ, and Furzy Cliff, near Weymouth, Dorset.

DIMENSIONS. From sample OC–Ox–PaR–52.

		Length	Height
Male L.V.	Io.5144	0·52	0·27

DESCRIPTION. Small to medium. Dimorphic. Anterior margin rounded ; posterior pointed with apex above mid-height. Left valve larger than right with dorsal overlap. Dorsal margin long and straight, or with slight median concavity ; ventral margin strongly upturned posteriorly. Sculpture of broad ribs and swellings. A broad rib extends ventrally from the anterior cardinal angle to an antero-ventral position, where it expands and increases in height. Dorsal to this is a vertically inclined median sulcus separating two large swellings. The intervening areas are punctate, weakly reticulate, or covered with very small ribs, especially on the caudal process where they are vertically aligned. Internal features typical of the genus.

REMARKS. This species, which is left here with open nomenclature because of insufficiency of material, is evidently very rare, two earlier records are from the *mariae* zone of Villers-sur-Mer (Bizon 1959) and of Warboys, Huntingdonshire (Glashoff 1964).

Genus ***PSEUDOPERISSOCYTHERIDEA*** Mandelstam 1960

REMARKS. This genus has been discussed by Brand & Malz (1962, pp. 25), and included in it by them, apart from the type (*Protocythere crassula* Mandelstam 1947) are three American species, *Progonocythere hieroglyphica* and *P. crowcreekensis* Swain & Peterson 1951 and *P. anoda* Peterson 1954, all from the Callovian and Oxfordian of the N. and N.W. United States. They also place here *Palaeocytheridea nikitina* and *P. milanovki* Lyubimova 1955, from the Lower Callovian of Russia. The present writer would prefer to consider *Progonocythere crowcreekensis* Swain & Peterson, as a species of *Fuhrbergiella*, to which its roughly reticulate ornament and sub-central tubercule would tend to ally it, rather than to the genus under consideration here. *Pseudoperissocytheridea parahieroglyphica* n. sp., described below has a surface sculpture mid-way between the costate American and the reticulate Russian forms.

Pseudoperissocytheridea parahieroglyphica n. sp.

Plate 15. Figs. 17, 19, 22–33.

DIAGNOSIS. Species of *Pseudoprissocytheridea* with surface sculpture consisting of a series of ' U ' shaped ribs which enclose a median area of more irregular ribs.

HOLOTYPE. One female L.V., HU.20.J.13, sample OC–Ox–Fy–5, *cordatum* zone, Furzy Cliff, Nr. Weymouth, Dorset.

DERIVATO NOMINIS. From its similarity to *P. hieroglyphica* (Swain & Peterson 1951).

DISTRIBUTION. In Scotland occurring in the *mariae* and *cordatum* zones at Port-an-Righ, and in the *cordatum* zone at Staffin Bay. It also occurs at a number of localities in the south of England where it ranges from the *mariae* to the *plicatilis* zone.

DIMENSIONS.

		Length	Height	Width
HOLOTYPE				
Female L.V.	HU.20.J.13	0·47	0·25	0·13
PARATYPES	From the same sample as the holotype.			
Female L.V.	Io.5145	0·45	0·24	0·15
Female R.V.	Io.5146	0·48	0·25	0·13
Male L.V.	Io.5147	0·55	0·27	0·15
Male R.V.	Io.5148	0·52	0·23	0·15
Female Carapace	Io.5149	0·55	0·25	0·27

DESCRIPTION. Medium. Subrectangular, thin-shelled. Left valve larger than right with dorsal and ventral overlap. Anterior margin of right valve rounded, with angle above mid-height and extremity at, or near mid-height ; left valve more angular. Anterior cardinal angle more pronounced in left than in right valves. Posterior margin pointed with apex above mid-height. Postero-ventral slope convex in both valves ; postero-dorsal slope concave in right and straight or convex in left. Ventral margin straight, upturned posteriorly. These margins converge more strongly posteriorly in right than in left valves, greatest height at the anterior cardinal angle ; width, in the posterior third. Sculpture consists of an irregular pattern of small thin ridges. Medially these ridges produce a coarsely reticulate pattern. Posteriorly, a group of 3–5 of these ridges extend vertically from the posterior cardinal angle to a postero-ventral position where they change direction through 90° and extend along the ventro-lateral surface to an antero-ventral position where they coalesce. They then change direction again through 90° and extend dorsally towards the anterior cardinal angle. Both anteriorly and posteriorly, these ribs form the junction between the highly ornamented lateral surface and the smooth marginal borders. A ridge borders the anterior margin and extends to a mid-ventral position. The extremity of the anterior margin is formed by a frill-like flange. A small ridge extends across the caudal process. Eye spot small and very close to the anterior cardinal angle. Normal pore canals few, large and circular. Marginal areas rather wide. The inner margin and line of concrescence usually coincide

throughout, but may diverge slightly anteriorly and or postero-ventrally. Radial pore canals straight, evenly spaced ; 8 anteriorly and 4 posteriorly. Hinge antimerodont. In the right valve, the terminal elements are raised dentate ridges with 5 teeth anteriorly and 7 posteriorly ; in both cases the teeth increase in size and height distally. The median element is a locellate groove. Complementary structures occur in the left valve hinge above which is a shelf-like accommodation groove. There are 4, vertically aligned adductors, anterior scars not seen. Sexual dimorphism pronounced ; male valves more elongate than female.

REMARKS. This species most closely resembles *P. hieroglyphica* (Swain & Peterson 1951) from the Redwater Shale member of the Morrison Formation of S. Dakota ; this falls within the *Cardioceras* (*Scarburgiceras*) *codiforme* zone which, according to Imlay, (1947, p. 261) is equivalent to the *mariae* zone of N.W. Europe. The present species differs from *Pseudoperissocytheridea hieroglyphica* in its less well defined ornament. The series of ribs which surround the median area on three sides are better developed in *P. hieroglyphica* and the ribs of the median area are stronger and more vertical in aspect. The present species is also smaller. From the two Russian species, *P. nitikina* and *P. milanovski* (Lyubimova 1955), *P. parahieroglyphica* n. sp. differs in possessing costate rather than reticulate ornament dorso-medianly.

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V. APPENDIX

The ostracods on which this paper is based were originally deposited in the collections of the Geology Department of Hull University. A large part of this collection has since been transferred to the British Museum (Natural History). The revised registration numbers are listed below :

British Museum Nos.	Hull University Nos.	British Museum Nos.	Hull University Nos.
Io.5030	Hu–16–J–4	Io.5046	Hu–17–J–11
Io.5031	Hu–16–J–6	Io.5047	Hu–17–J–12
Io.5032	Hu–16–J–7	Io.5048	Hu–17–J–28
Io.5033	Hu–16–J–8	Io.5049	Hu–17–J–29
Io.5034	Hu–16–J–9	Io.5050	Hu–17–J–30
Io.5036	Hu–16–J–12	Io.5051	Hu–17–J–31
Io.5037	Hu–16–J–13	Io.5052	Hu–17–J–32
Io.5038	Hu–16–J–24	Io.5053	Hu–17–J–33
Io.5039	Hu–16–J–25	Io.5054	Hu–17–J–34
Io.5040	Hu–16–J–31	Io.5055	Hu–17–J–35
Io.5041	Hu–16–J–40	Io.5056	Hu–17–J–36
Io.5042	Hu–17–J–7	Io.5057	Hu–17–J–40
Io.5043	Hu–17–J–8	Io.5058	Hu–18–J–9
Io.5044	Hu–17–J–9	Io.5059	Hu–18–J–10
Io.5045	Hu–17–J–10	Io.5060	Hu–18–J–12

British Museum Nos.	Hull University Nos.	British Museum Nos.	Hull University Nos.
Io.5061	Hu–18–J–13	Io.5106	Hu–19–J–77
Io.5062	Hu–18–J–14	Io.5107	Hu–19–J–78
Io.5063	Hu–18–J–15	Io.5108	Hu–19–J–79
Io.5064	Hu–18–J–16	Io.5109	Hu–19–J–81
Io.5065	Hu–18–J–17	Io.5110	Hu–19–J–82
Io.5066	Hu–18–J–19	Io.5111	Hu–19–J–83
Io.5067	Hu–18–J–20	Io.5112	Hu–19–J–84
Io.5068	Hu–18–J–31	Io.5113	Hu–19–J–85
Io.5069	Hu–18–J–32	Io.5114	Hu–19–J–87
Io.5070	Hu–18–J–33	Io.5115	Hu–19–J–88
Io.5071	Hu–18–J–41	Io.5116	Hu–19–J–67
Io.5072	Hu–18–J–42	Io.5117	Hu–19–J–68
Io.5073	Hu–18–J–43	Io.5118	Hu–19–J–103
Io.5074	Hu–18–J–44	Io.5119	Hu–19–J–104
Io.5075	Hu–18–J–45	Io.5120	Hu–19–J–105
Io.5076	Hu–18–J–51	Io.5121	Hu–19–J–106
Io.5077	Hu–18–J–52	Io.5122	Hu–19–J–107
Io.5078	Hu–18–J–53	Io.5123	Hu–20–J–11
Io.5079	Hu–18–J–38	Io.5124	Hu–20–J–12
Io.5080	Hu–18–J–39	Io.5125	Hu–20–J–21
Io.5081	Hu–18–J–59	Io.5126	Hu–20–J–23
Io.5082	Hu–19–J–13	Io.5127	Hu–20–J–24
Io.5083	Hu–19–J–14	Io.5128	Hu–20–J–25
Io.5084	Hu–19–J–15	Io.5129	Hu–20–J–26
Io.5085	Hu–17–J–42	Io.5130	Hu–20–J–27
Io.5086	Hu–17–J–43	Io.5131	Hu–20–J–29
Io.5087	Hu–17–J–44	Io.5132	Hu–20–J–30
Io.5088	Hu–16–J–62	Io.5133	Hu–20–J–31
Io.5089	Hu–19–J–34	Io.5134	Hu–20–J–33
Io.5090	Hu–19–J–35	Io.5135	Hu–20–J–34
Io.5091	Hu–19–J–36	Io.5136	Hu–20–J–35
Io.5092	Hu–19–J–37	Io.5137	Hu–20–J–36
Io.5093	Hu–19–J–38	Io.5138	Hu–20–J–37
Io.5094	Hu–19–J–39	Io.5139	Hu–20–J–38
Io.5095	Hu–19–J–42	Io.5140	Hu–20–J–67
Io.5096	Hu–19–J–45	Io.5141	Hu–20–J–68
Io.5097	Hu–19–J–46	Io.5142	Hu–20–J–69
Io.5098	Hu–19–J–47	Io.5143	Hu–20–J–70
Io.5099	Hu–19–J–70	Io.5144	Hu–20–J–71
Io.5100	Hu–19–J–71	Io.5145	Hu–20–J–14
Io.5101	Hu–19–J–72	Io.5146	Hu–20–J–15
Io.5102	Hu–19–J–73	Io.5147	Hu–20–J–16
Io.5103	Hu–19–J–74	Io.5148	Hu–20–J–17
Io.5104	Hu–19–J–75	Io.5149	Hu–20–J–18

ADDENDUM

Since this paper was written, the author has changed his opinion concerning the status of *Glabellacythere dolabra* (Jones & Sherborn) and *Glabellacythere nuda* Wienholz. Dr. R. H. Bate has examined topotypic material of the latter and has satisfied the author that they are distinct species. The species here described as *G. dolabra* should now be identified as *G. nuda* Wienholz. A more complete taxonomic comment on this will appear in a later publication.

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PLATE 1

Polycope pelta Fischer 1961 p.

FIGS. 1–4. Carapace (Io.5030) × 58
1. Left lateral view
2. Dorsal view
3. Ventral view
4. Right lateral view

Polycope sububiquita n. sp. p.

FIGS. 5–7, 10. Carapace (HU.16.J.5), holotype. × 60
5. Right lateral view
6. Dorsal view
7. Ventral view
10. Left lateral view

FIGS. 8, 9, 11, 15. Carapace (Io.5032), paratype. × 60
8. Dorsal view
9. Ventral view
11. Right lateral view
15. Left lateral view

Cytherella fullonica Jones and Sherborn 1888 p.

FIGS. 12, 16. Left valve (Io.5036) × 55
12. External view
16. Internal view

FIGS. 13, 14, 18 Carapace (Io.5037) × 55
13. Dorsal view
14. Ventral view
18. Left lateral view

Macrocypris aequabilis Oertli 1959 p.

FIGS. 17, 19. Right valve (Io.5038) × 62
17. External view
19. Internal view

FIGS. 21, 26. Carapace (Io.5039) × 62
21. Left lateral view
26. Dorsal view

Paracypris sp. A. p.

FIGS. 20, 22, 23, 29. Carapace (HU.16.J.29) × 40
20. Left lateral view
22. Right lateral view
23. Dorsal view
29. Ventral view

Argilloecia sp. A. p.

FIGS. 24, 25, 27, 28. Carapace (Io.5040) × 52
24. Right lateral view
25. Dorsal view
27. Ventral view
28. Left lateral view

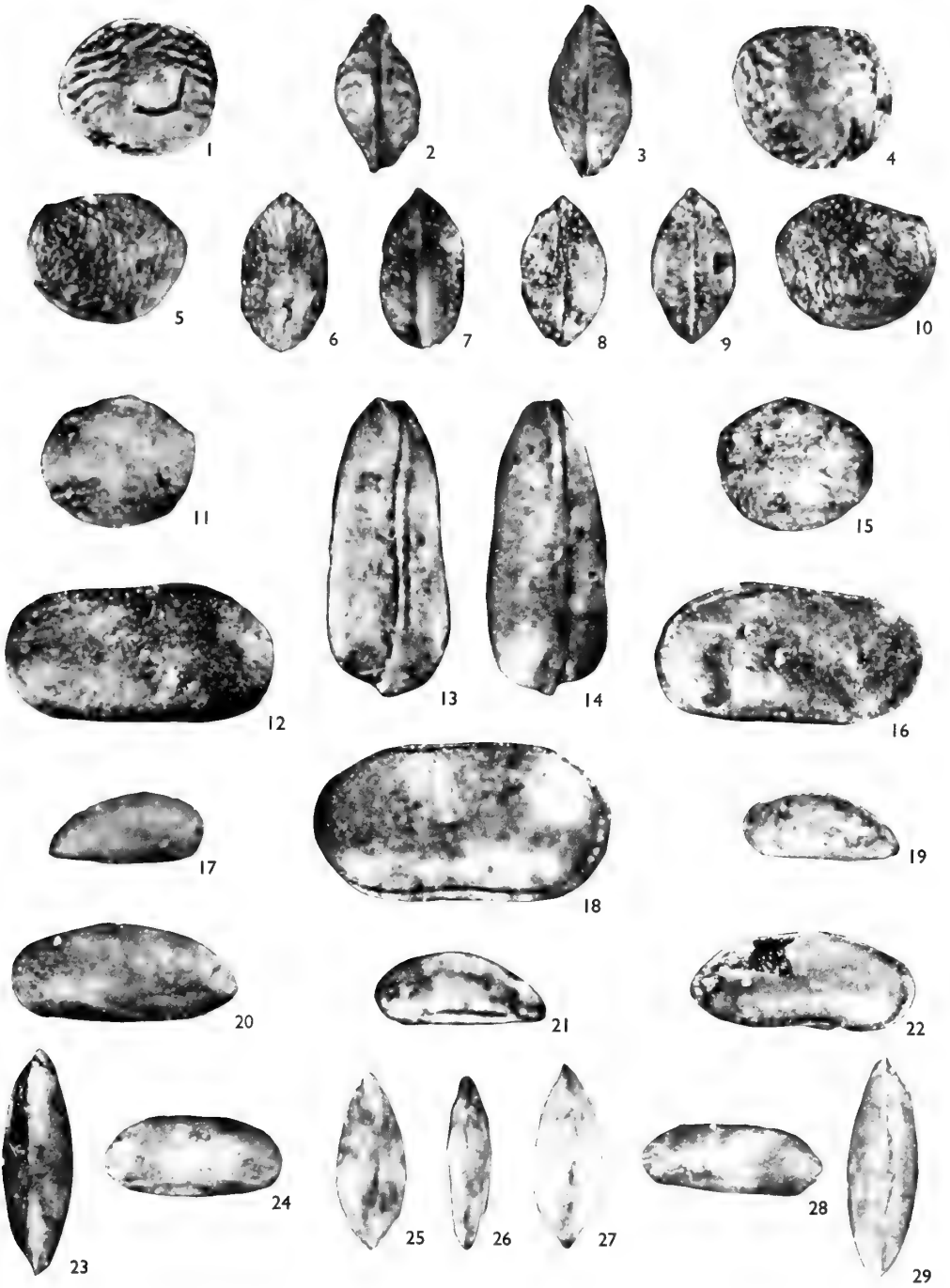
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PLATE 2

Krausella sp. A. p.

FIGS. 1, 2, 5, 6. Carapace (Io.5041) × 55
1. Left lateral view
2. Dorsal view
5. Ventral view
6. Right lateral view

Caytonidea terraefullonicae (Jones and Sherborn 1888) p.

FIGS. 7, 8. Left valve (Io.5088) × 55
7. External view
8. Internal view

Praeschuleridea batei n. sp. p.

FIGS. 4, 9–10, 11. Male right valve (HU.17.J.6), holotype × 52
4. Dorsal view
9. Internal view in transmitted light
10. External view
11. Internal view

FIGS. 3, 12–14. Male left valve (Io.5043), paratype × 52
3. Dorsal view
12. Internal view, transmitted light
13. External view
14. External view transmitted light

FIGS. 15. Female right valve (Io.5044), paratype × 52
15. External view

FIGS. 16, 18, 20, 22. Female carapace (Io.5046), paratype × 52
16. Right lateral view
18. Dorsal view
20. Left lateral view
22. Ventral view

FIG. 17. Female left valve (Io.5045), paratype × 52

FIGS. 19, 21. Male carapace (Io.5047), paratype × 52
19. Dorsal view
21. Ventral view

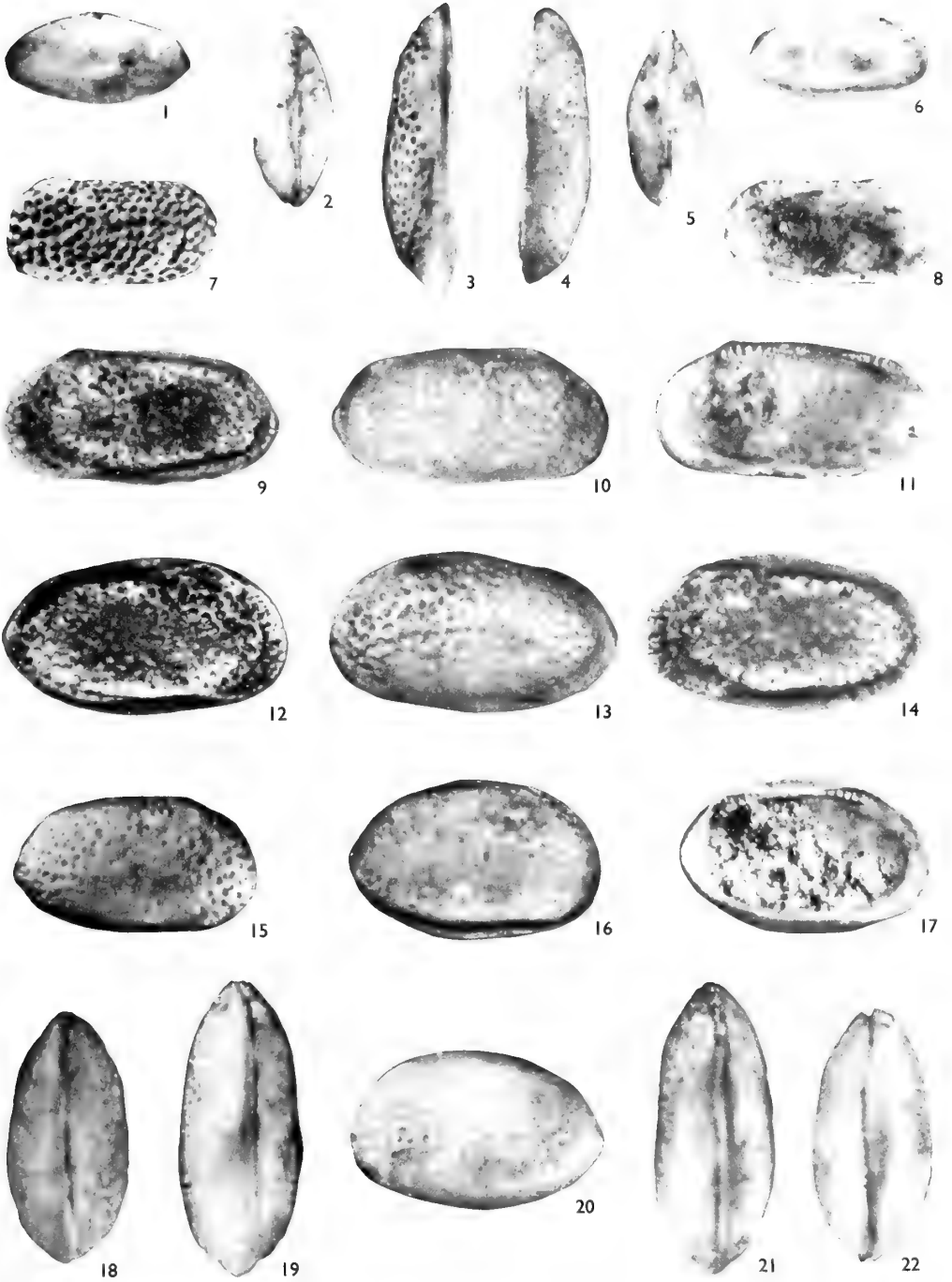
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PLATE 3

Monoceratina scrobiculata Triebel and Bartenstein 1938 p.

FIGS. 1, 3, 4. Right valve (Io.5048) × 54
1. External view
3. Dorsal view
4. External view in transmitted light

FIGS. 2, 5, 6, 10. Left valve (Io.5049) × 54
2. Dorsal view
5. Internal view
6. External view
10. External view in transmitted light

FIGS. 7, 9. Carapace (Io.5050) × 54
7. Right lateral view
9. Dorsal view

Monoceratina stimulea (Schwager 1866) p.

FIGS. 8, 11, 14. Right valve (Io.5051) × 56
8. Dorsal view
11. External view
14. Internal view

FIGS. 15, 16. Left valve (Io.5052) × 56
15. External view in transmitted light
16. External view

FIGS. 12, 13, 17. Carapace (Io.5053) × 56
12. Dorsal view
13. Ventral view
17. Left lateral view

Monoceratina vulsa (Jones and Sherborn 1888) p.

FIGS. 18, 20, 21. Right valve (Io.5054) × 60
18. External view
20. Dorsal view
21. Internal view

FIGS. 19, 22, 24. Left valve (Io.5055) × 60
19. Dorsal view
22. External view
24. Internal view

FIGS. 23, 25. Carapace (Io.5056) × 60
23. Dorsal view
25. Ventral view

Monoceratina sp. A. p.

FIGS. 26. Broken left valve (Io.5057) × 60

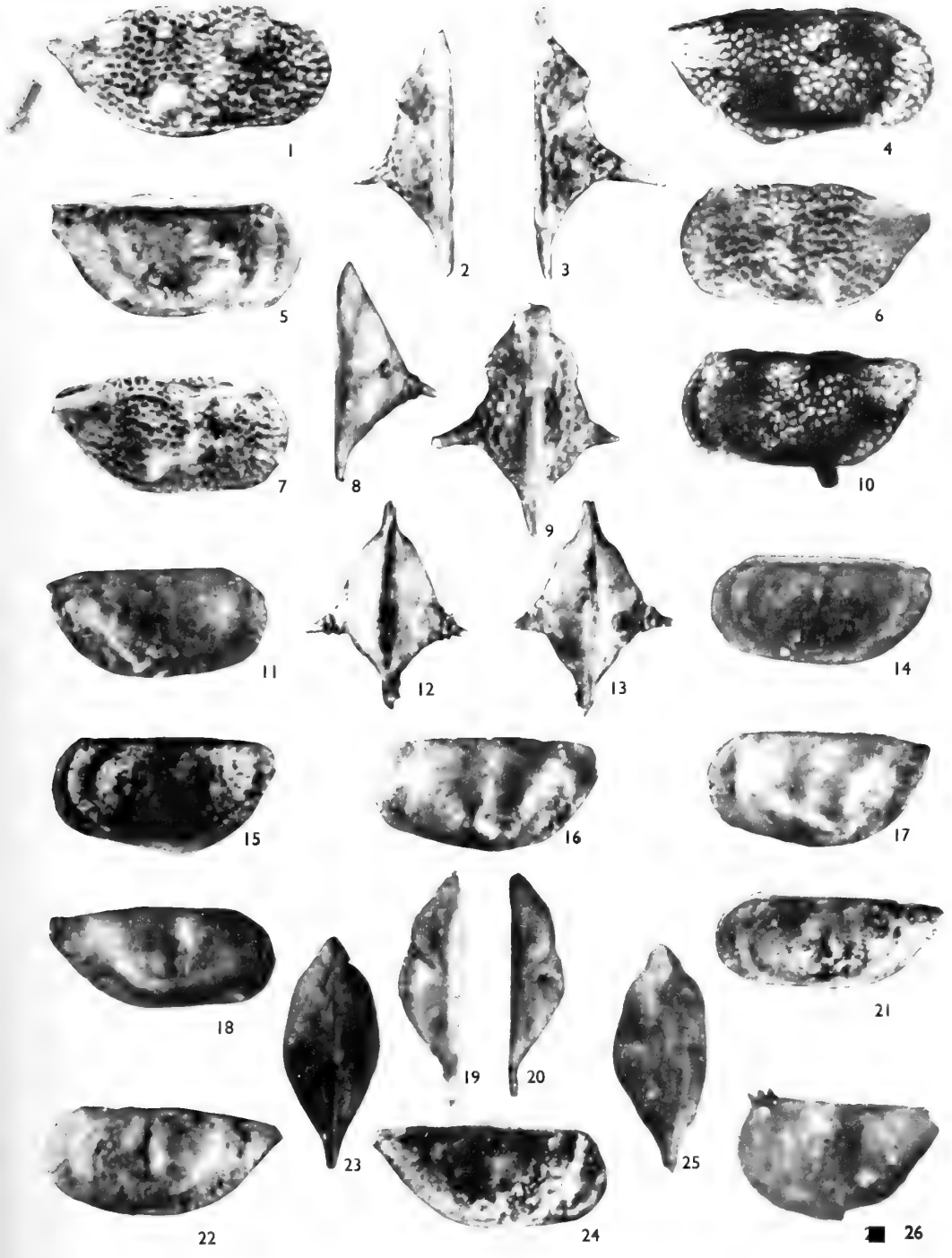
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PLATE 4

Galliaecytheridea staffinensis n. sp. p.

FIGS. 1–3. Carapace (HU.18.J.8), holotype × 64
1. Right lateral view
2. Dorsal view
3. Left lateral view

FIG. 4. Broken left valve (Io.5059), paratype × 64
4. Internal view through glycerin

FIGS. 5, 6. Carapace (Io.5058), paratype × 64
5. Dorsal view
6. Left lateral view

Glabellacythere reticulata sp. n. p.

FIGS. 7–10. Female Carapace (HU.18.J.11), holotype × 62
7. Dorsal view
8. Ventral view
9. Left lateral view
10. Right lateral view

FIGS. 11, 17. Female left valve (Io.5061), paratype × 62
11. Dorsal view
17. External view

FIGS. 12, 13, 16. Female right valve (Io.5060), paratype ×62
12. Dorsal view
13. Internal view
16. External view

FIG. 14. Male left valve (Io.5063), paratype × 62
14. Dorsal view

FIG. 15. Male right valve (Io.5062), paratype × 62
15. Dorsal view

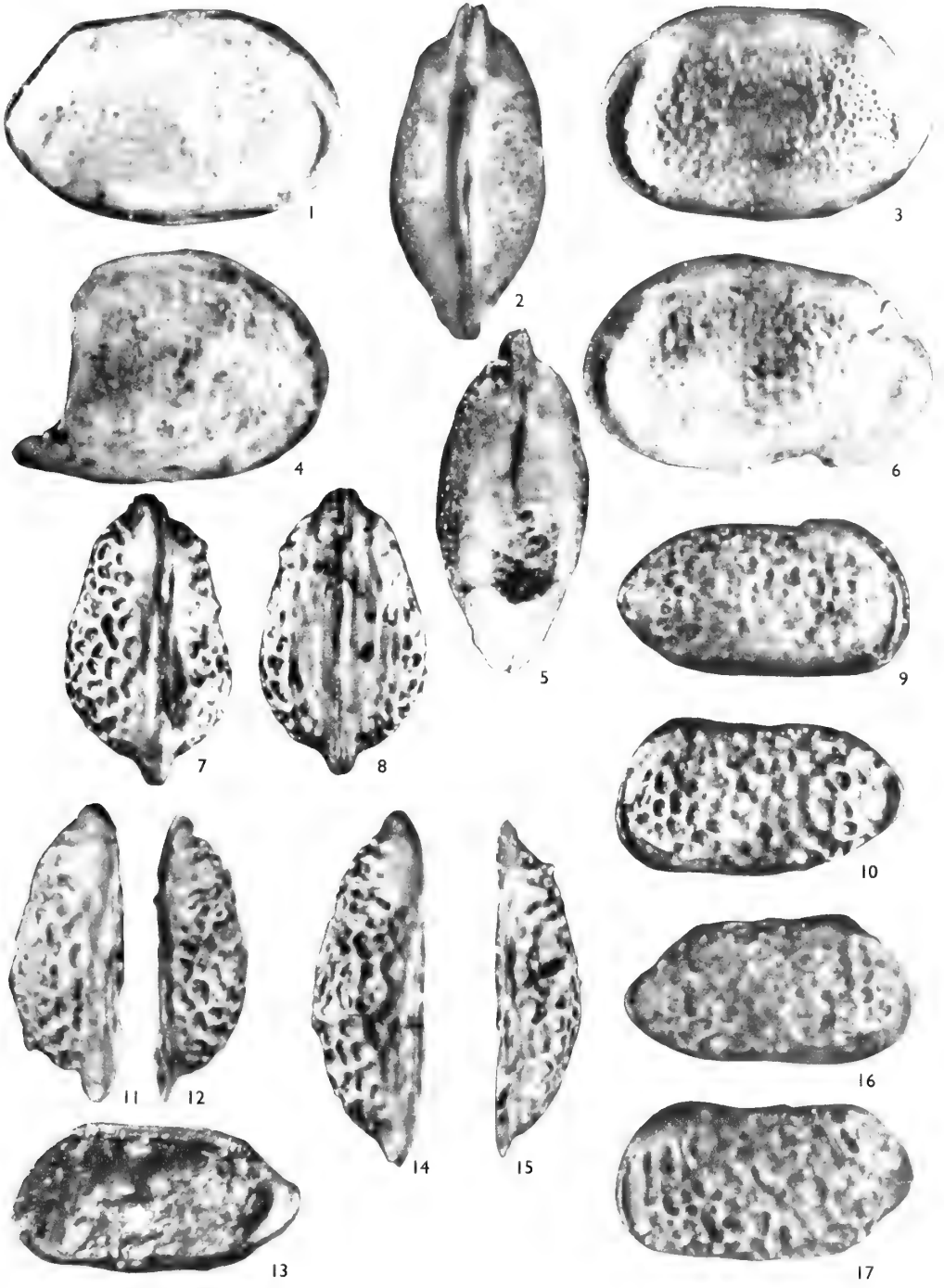
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PLATE 5

Glabellacythere reticulata sp. n. p.

FIGS. 1, 2. Male left valve (Io.5063), paratype × 62
1. External view
2. Internal view

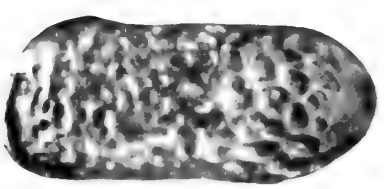
FIGS. 3–6. Male carapace (Io.5064), paratype × 62
3. Left lateral view
4. Dorsal view
5. Right lateral view
6. Ventral view

Glabellacythere dolabra (Jones and Sherborn) p.

FIGS. 7, 9, 11, 12. Right valve (HU.18.J.17), holotype
7. External view in transmitted light × 68
9. External view × 60
11. Dorsal view × 60
12. Internal view × 60

FIGS. 8, 10, 13, 14. Left valve (Io.5066), paratype
8. External view in transmitted light × 68
10. Dorsal view × 60
13. External view × 60
14. Internal view × 60

FIGS. 15–18. Carapace (Io.5067), paratype × 60
15. Left lateral view
16. Dorsal view
17. Ventral view
18. Right lateral view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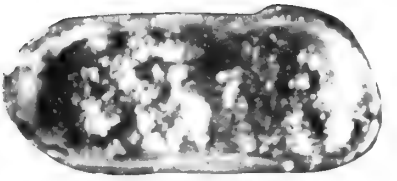
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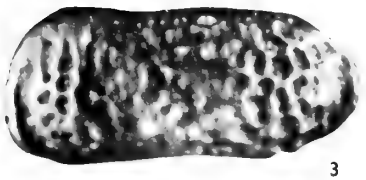
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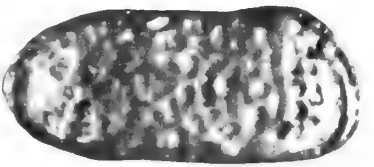
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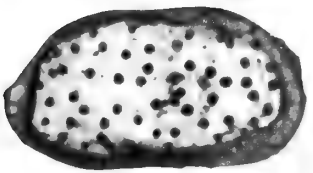
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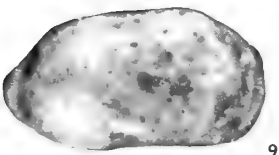
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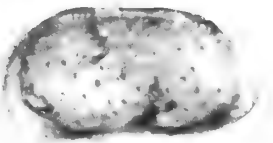
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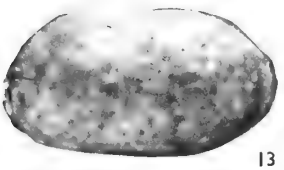
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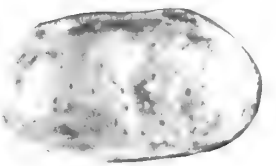
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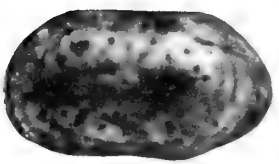
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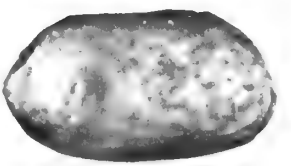
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PLATE 6

Procytherura tenuicostata Gen. et. sp. n. p.

FIGS. 1–3. Left valve (HU.18.J.30), holotype ×80
1. External view
2. Dorsal view
3. Internal view

FIGS. 4, 8. Carapace (HU.18.J.34), paratype × 80
4. Dorsal view
8. Right lateral view

FIGS. 5, 6. Right valve (Io.5069), paratype × 80
5. External view
6. Internal view

FIG. 7. Right valve (Io.5068), paratype × 80

Eucytherura (Vesticytherura) costaeirregularis n. sp. p.

FIGS. 9, 10, 12. Left valve (HU.18J.40), holotype × 90
9. External view
10. Dorsal view
12. Internal view

FIGS. 11, 13, 14. Right valve (Io.5074), paratype × 90
11. Dorsal view
13. External view
14. Internal view

FIG. 15. Left valve (Io.5073), paratype × 90

FIGS. 16, 17. Carapace (Io.5075), paratype × 90
16. Dorsal view
17. Ventral view

FIG. 18. Right valve (Io.5071), paratype ×90

FIGS. 19, 21. Left valve (Io.5072), paratype × 90
19. External view
21. Internal view

Eucytherura (Vesticytherura) horrida n. sp. p.

FIG. 20. Left valve (HU.18.J.50), holotype × 100

FIG. 22. Left valve (Io.5076), paratype × 100

FIGS. 23, 24. Right valve (Io.5077), paratype × 100
23. External view
24. Internal view

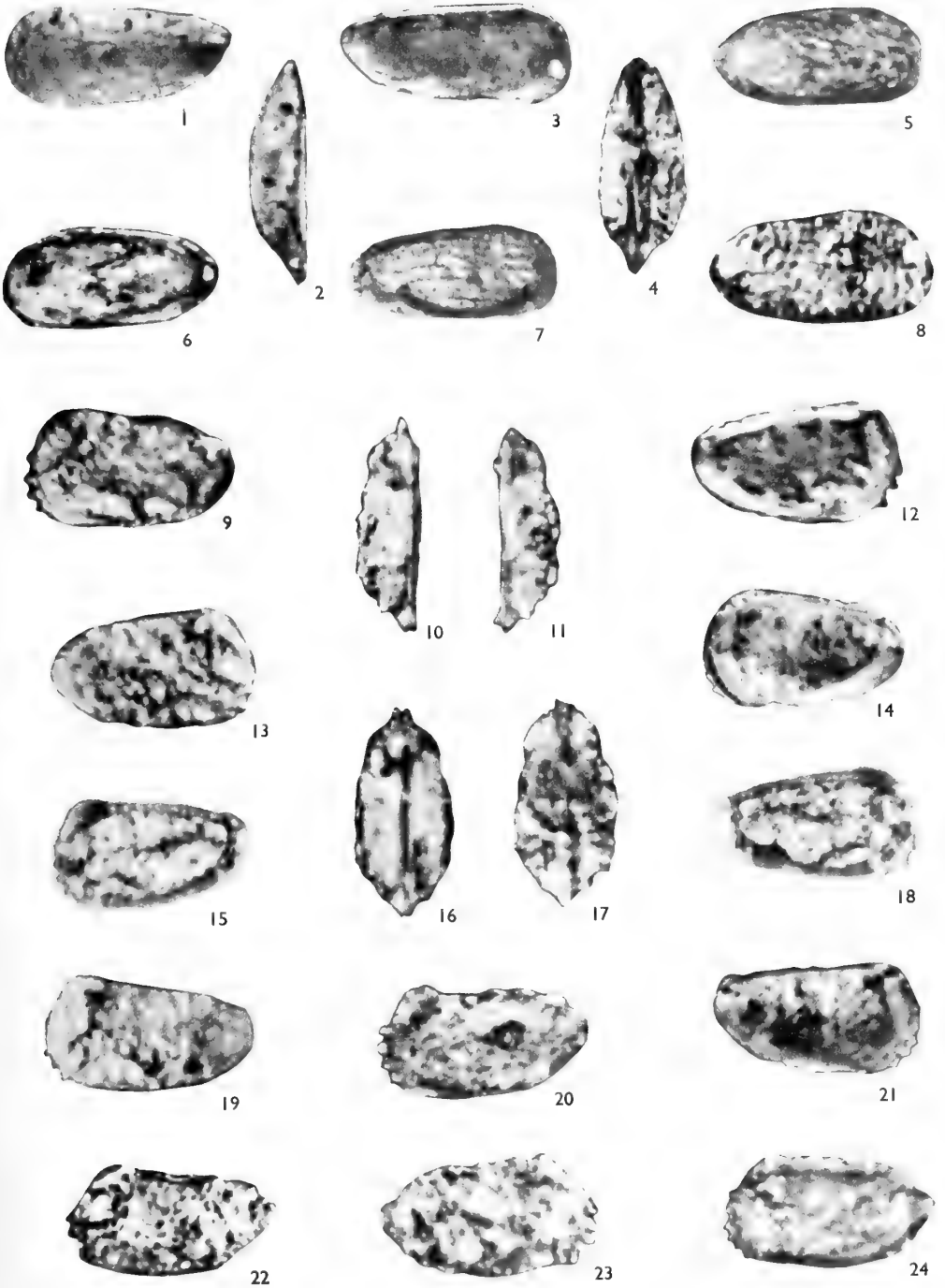
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PLATE 7

Eucytherura (Vesticytherura) horrida n. sp. p.

FIGS. 1, 2, 5, 6. Carapace (Io.5078), paratype × 100
1. Left lateral view
2. Dorsal view
5. Ventral view
6. Right lateral view

FIG. 3. Left valve (HU.18.J.50), holotype × 100
3. Dorsal view

FIG. 4. Right valve (Io.5077), paratype × 100

Eucytherura (Vesticytherura) scottia n. sp. p.

FIGS. 7, 8, 11. Left valve (HU.18.J.37), holotype × 85
7. External view
8. Internal view
11. Dorsal view

FIGS. 9, 10, 12, 13. Carapace (Io.5079), paratype × 85
9. Left lateral view
10. Dorsal view
12. Ventral view
13. Right lateral view

Cytheropteron aquitanum Donze 1960 p.

FIGS. 14–16. Left valve (Io.5081) × 90
14. Internal view
15. Dorsal view
16. External view

Metacytheropteron sutherlandensis n. sp. p.

FIGS. 17, 18, 23. Male right valve (HU.19.J.12), holotype × 94
17. External view
18. Internal view
23. Dorsal view

FIGS. 19, 20, 22. Male left valve (Io.5082), paratype × 94
19. External view
20. Internal view
22. Dorsal view

FIGS. 21, 24. Female left valve (Io.5083), paratype × 94
21. Internal view
24. External view

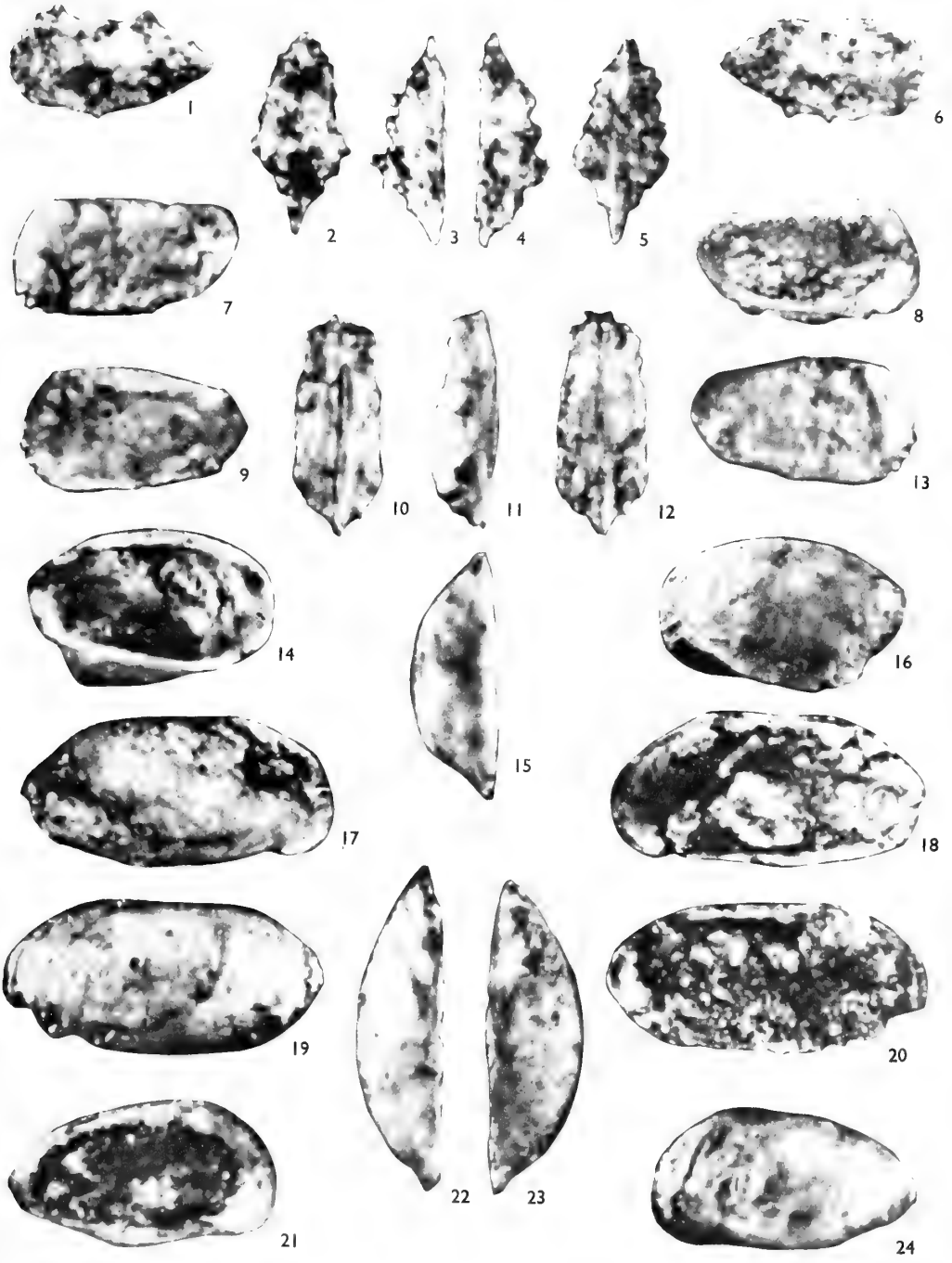
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PLATE 8

Metacytheropteron sp. A. p.

FIGS. 1–4. Carapace (Io.5084) × 92
1. Left lateral view
2. Dorsal view
3. Ventral view
4. Right lateral view

Pedicythere anterodentina n. sp

FIGS. 5, 6, 13. Right valve (HU.17.J.41), holotype × 84
5. External view
6. Internal view
13. Dorsal view

FIGS. 7, 8, 12. Left valve (Io.5085), paratype × 84
7. External view
8. Internal view
12. Dorsal view

FIGS. 9, 10, 11, 14. Carapace (Io.5086), paratype × 84
9. Right lateral view
10. Left lateral view
11. Dorsal view
14. Ventral view

Lophocythere (Lophocythere) scabra bucki Lutze 1960 p.

FIGS. 15, 17. Male right valve (Io. 5089) × 62
15. External view in transmitted light
17. Dorsal view

FIGS. 16, 18. Male left valve (Io.5090) × 62
16. Dorsal view
18. External view in transmitted light

FIGS. 19, 23. Male carapace (Io.5091) × 62
19. Left lateral view
23. Right lateral view

FIGS. 20, 21. Female left valve (Io.5092) × 62
20. External view in transmitted light
21. Internal view

FIG. 22. Female right valve (Io.5093) × 62
22. Internal view

FIG. 24. Female carapace (Io.5094) × 62
24. Right lateral view

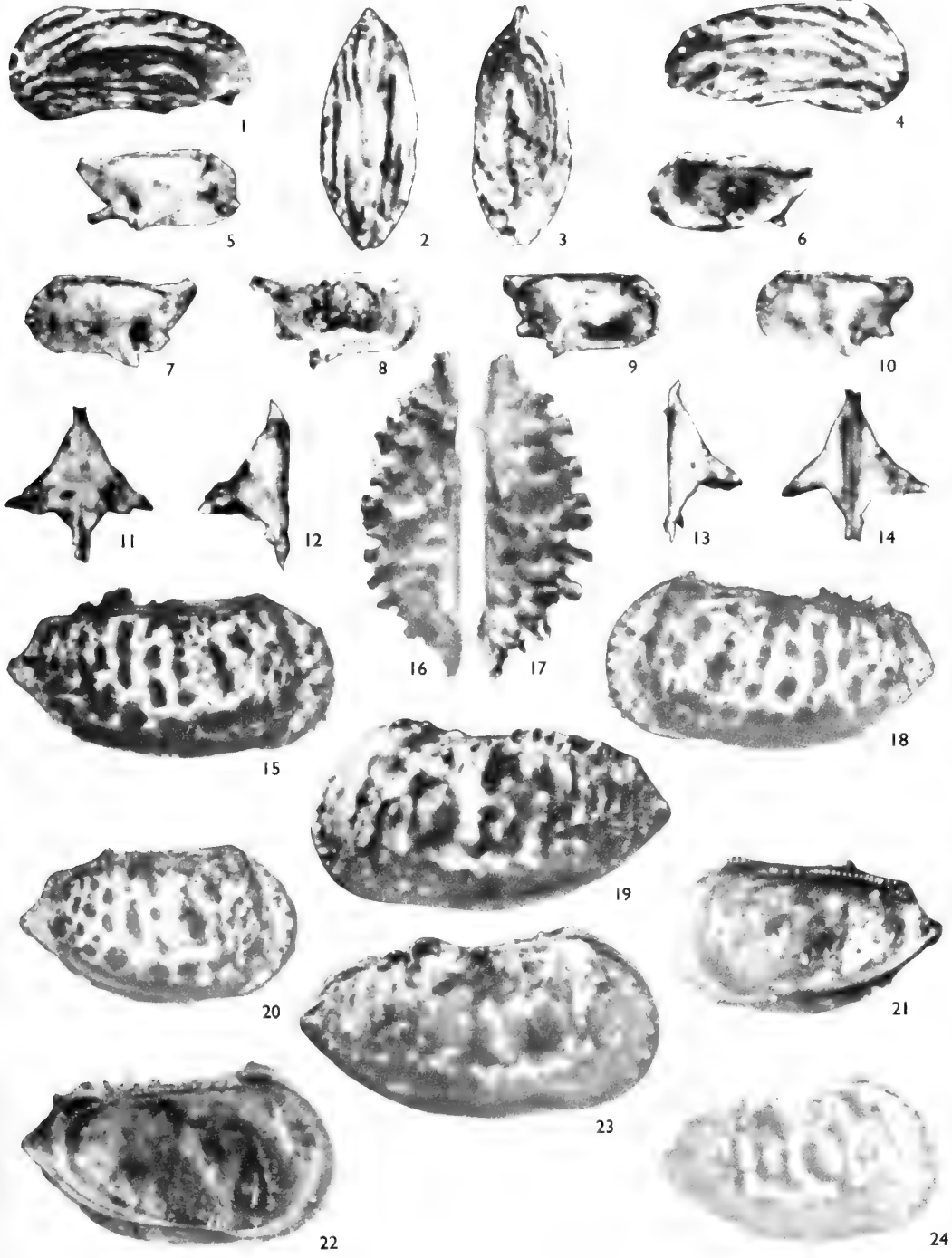
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PLATE 9

Lophocythere (Lophocythere) scabra bucki Lutze 1960 p.

FIGS. 1, 5. Male carapace (Io.5091) × 62
1. Dorsal view
5. Ventral view

Lophocythere (Lophocythere) interrupta interrupta Triebel 1951 p.

FIGS. 2, 3, 9. Male right valve (Io.5096) × 62
2. External view
3. Internal view
9. Dorsal view

FIGS. 4, 7. Female left valve (Io.5095) × 62
4. Dorsal view
7. Internal view

FIGS. 6, 10. Male carapace (Io.5097) × 62
6. Dorsal view
10. Ventral view

FIG. 8. Female carapace (Io.5098) × 62
8. Left lateral view

Lophocythere (Neurocythere) cruciata alata Subgen. et. Subsp. n. p.

FIGS. 11, 12, 16. Right valve (Io.5103), paratype × 64
11. External view
12. External view in transmitted light
16. Dorsal view

FIGS. 13–15. Left valve (HU.19.J.69), holotype × 64
13. External view
14. Internal view
15. Dorsal view

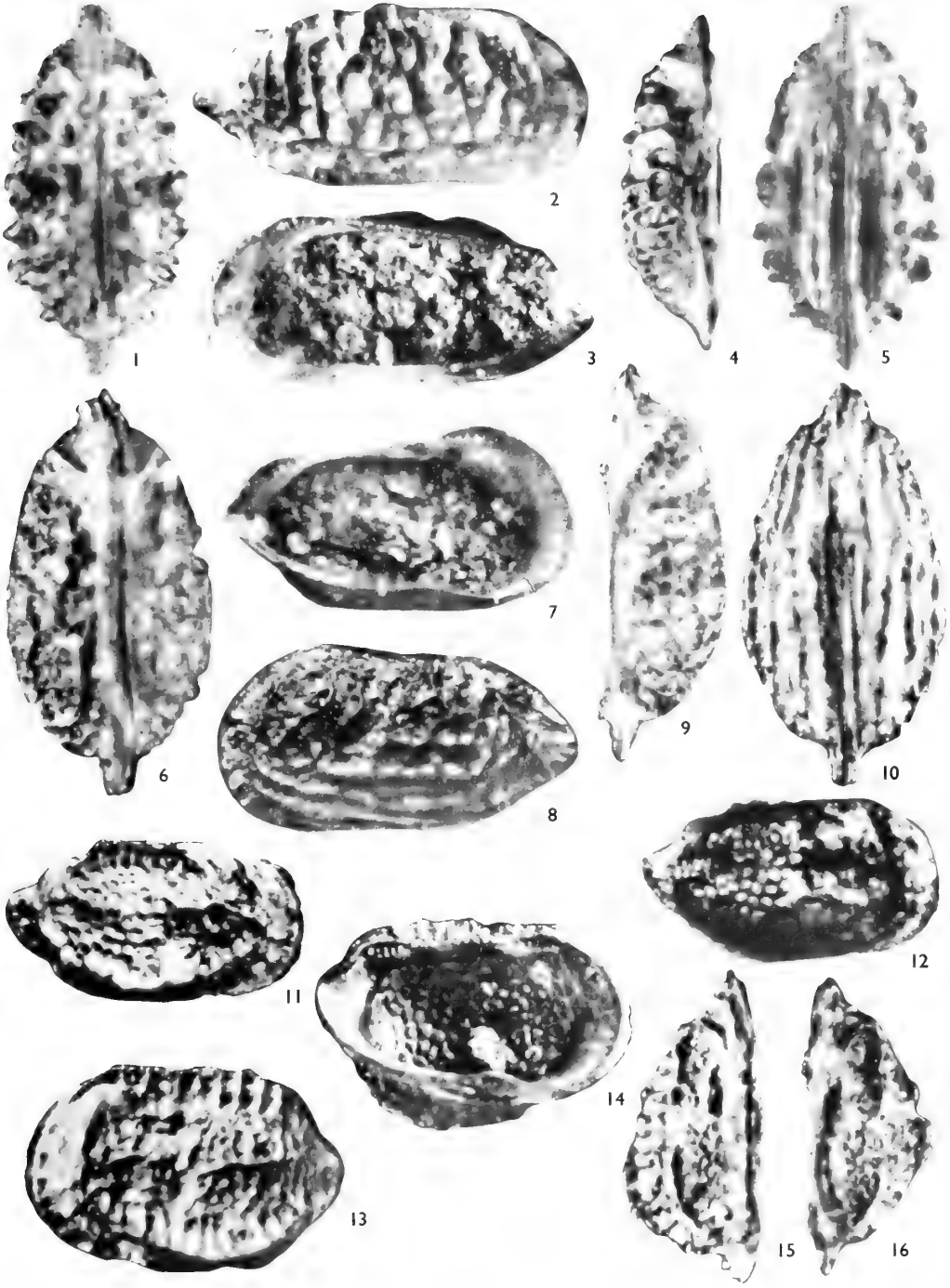
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PLATE 10

Lophocythere (Neurocythere) cruciata alata Subgen. et. sp. n. p.

FIG. 1. Left valve (Io.5100), paratype × 64
1. External view

FIGS. 2, 4, 5, 8. Carapace (HU.19.J.76), paratype × 64
2. Dorsal view
4. Left lateral view
5. Right lateral view
8. Ventral view

FIG. 3. Right valve (Io.5103), paratype × 64
3. Internal view

Lophocythere (Neurocythere) cruciata intermedia Lutze 1960 p.

FIGS. 6, 9, 10. Female right valve (Io.5106) × 62
6. External view
9. Dorsal view
10. Internal view

FIGS. 7, 11, 15. Female left valve (Io.5107) × 62
7. Dorsal view
11. External view
15. Internal view

FIGS. 12, 16, 17. Male right valve (Io.5108) × 62
12. Dorsal view
16. External view
17. Internal view

FIGS. 13, 14, 18, 19. Female carapace (Io.5109) × 62
13. Dorsal view
14. Ventral view
18. Right lateral view
19. Left lateral view

FIGS. 20, 21. Male carapace (Io.5110) × 62
20. Left lateral view
21. Right lateral view

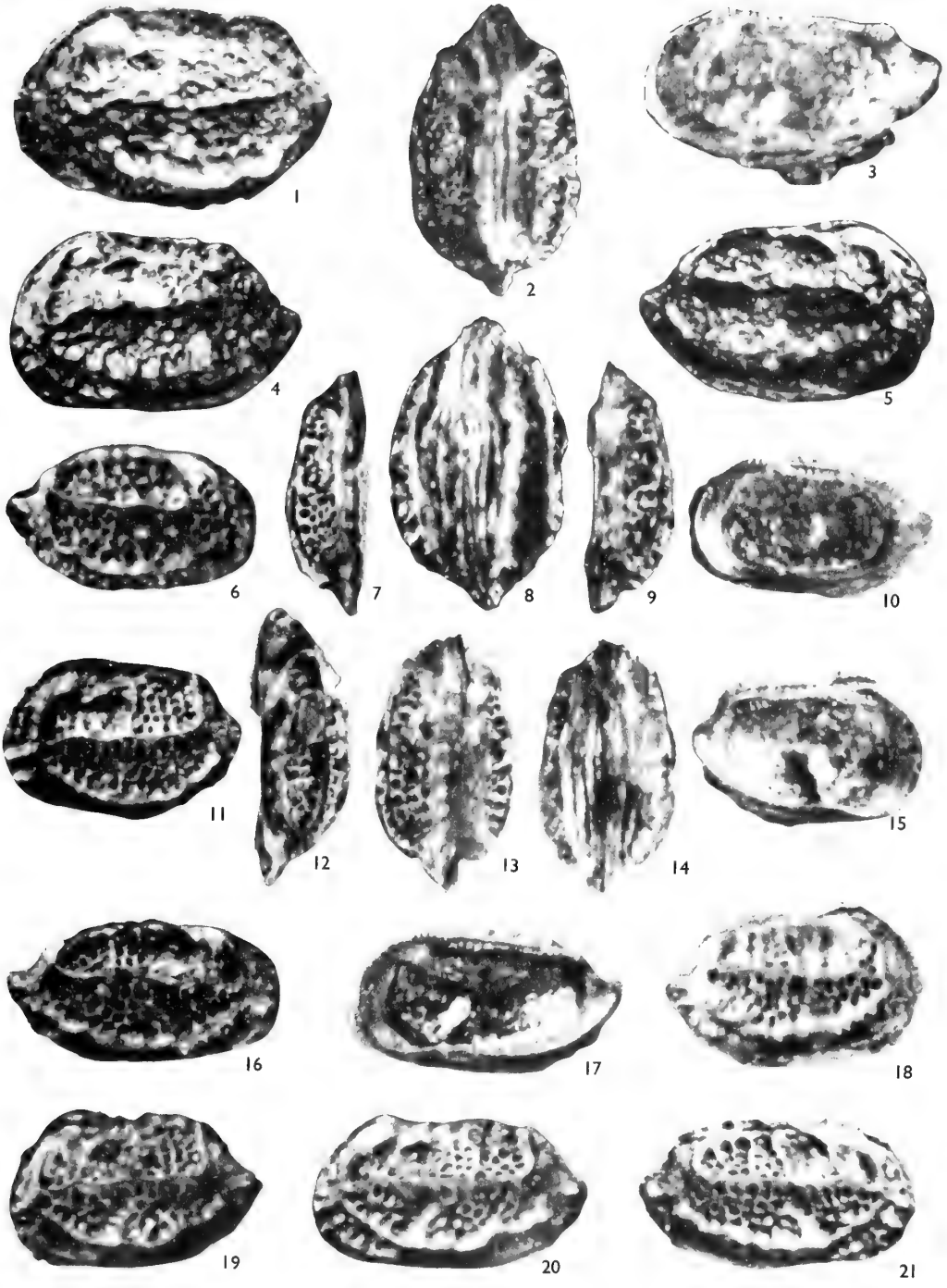
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PLATE 11

Lophocythere (Neurocythere) cruciata intermedia Lutze 1960 p.

FIGS. 1, 4. Male carapace (Io.5110) × 62
1. Dorsal view
4. Ventral view

Lophocythere (Neurocythere) cruciata oxfordiana Lutze 1960 p.

FIGS. 2, 3. Female right valve (Io.5111) × 64
2. External view
3. Internal view

FIGS. 5, 6. Female left valve (Io.5112) × 64
5. External view
6. Internal view

FIGS. 7, 8, 10, 12. Female carapace (Io.5114) × 64
7. Right lateral view
8. Left lateral view
10. Dorsal view
12. Ventral view

FIGS. 9, 13, 15, 16. Male carapace (Io.5115) × 64
9. Left lateral view
13. Right lateral view
15. Ventral view
16. Dorsal view

FIGS. 11, 14. Male right valve (Io.5113) × 64
11. Dorsal view
14. External view

FIG. 17. Male left valve (HU.19.J.86) × 64
17. External view

Lophocythere (Neurocythere) cruciata cruciata Triebel 1951 p.

FIGS. 18, 19, 21. Female left valve (Io.5116) × 64
18. Internal view
19. External view
20. Dorsal view

FIGS. 20, 22. Female carapace (Io.5117) × 64
20. Ventral view
22. Dorsal view

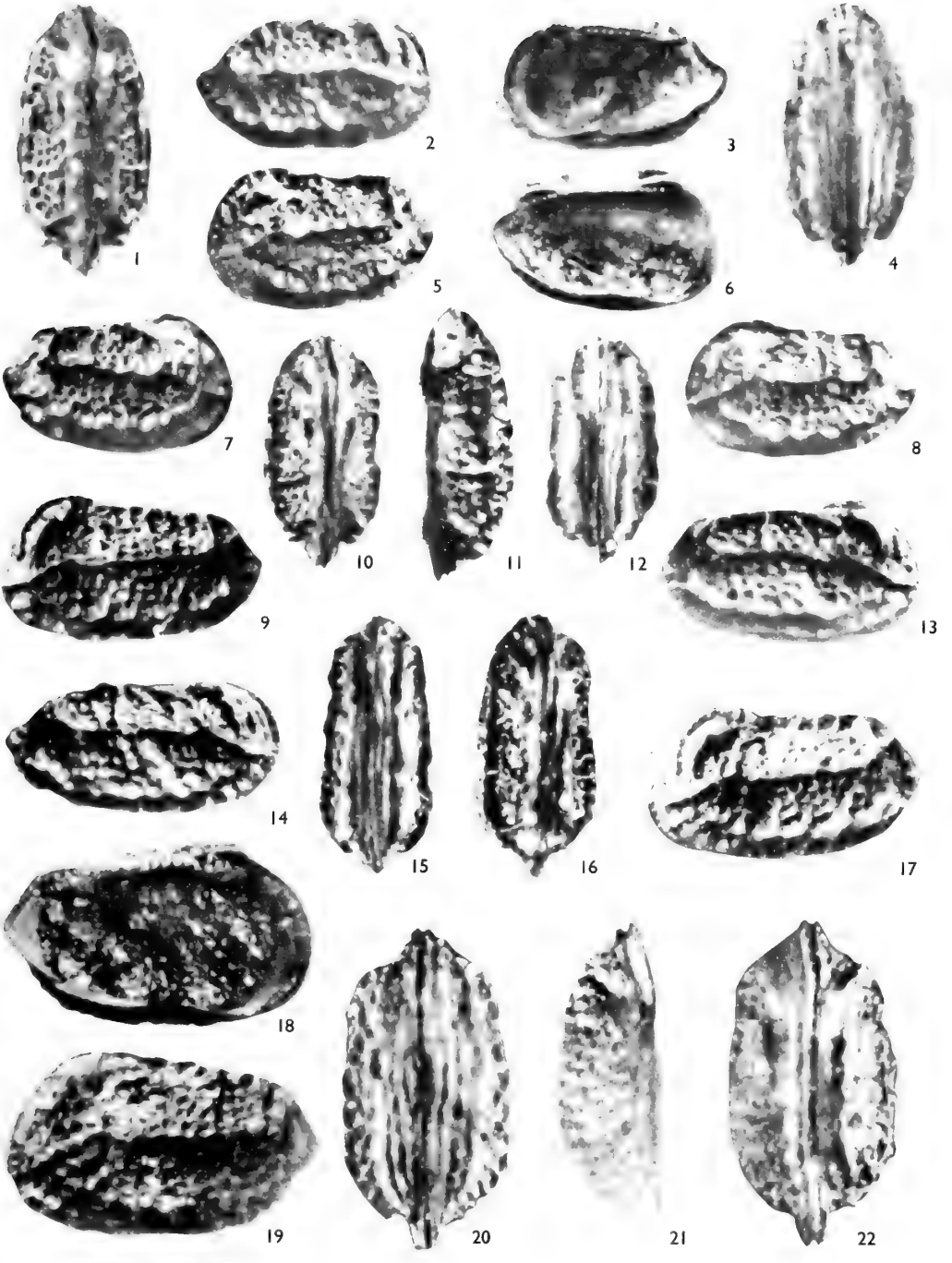
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PLATE 12

Lophocythere (Neurocythere) flexicosta lutzei Subgen. et. Subsp. n. p.

FIGS. 1–3. Female right valve (HU.19.J.102), holotype × 64
1. External view
2. Dorsal view
3. Internal view

FIG. 4. Male left valve (Io.5120), paratype × 64

FIG. 5. Male right valve (Io.5119), paratype × 64

FIGS. 6–8. Female carapace (Io.5122), paratype × 64
6. Left lateral view
7. Dorsal view
8. Right lateral view

FIGS. 9–12. Male carapace (Io.5121), paratype × 64
9. Dorsal view
10. Right lateral view
11. Left lateral view
12. Ventral view

Fuhrbergiella (Praefuhrbergiella) horrida horrida Brand and Malz 1962 p.

FIGS. 13, 15. Female carapace (Io.5123) × 62
13. Right lateral view
15. Left lateral view

FIG. 14. Male right valve (Io.5124) × 62

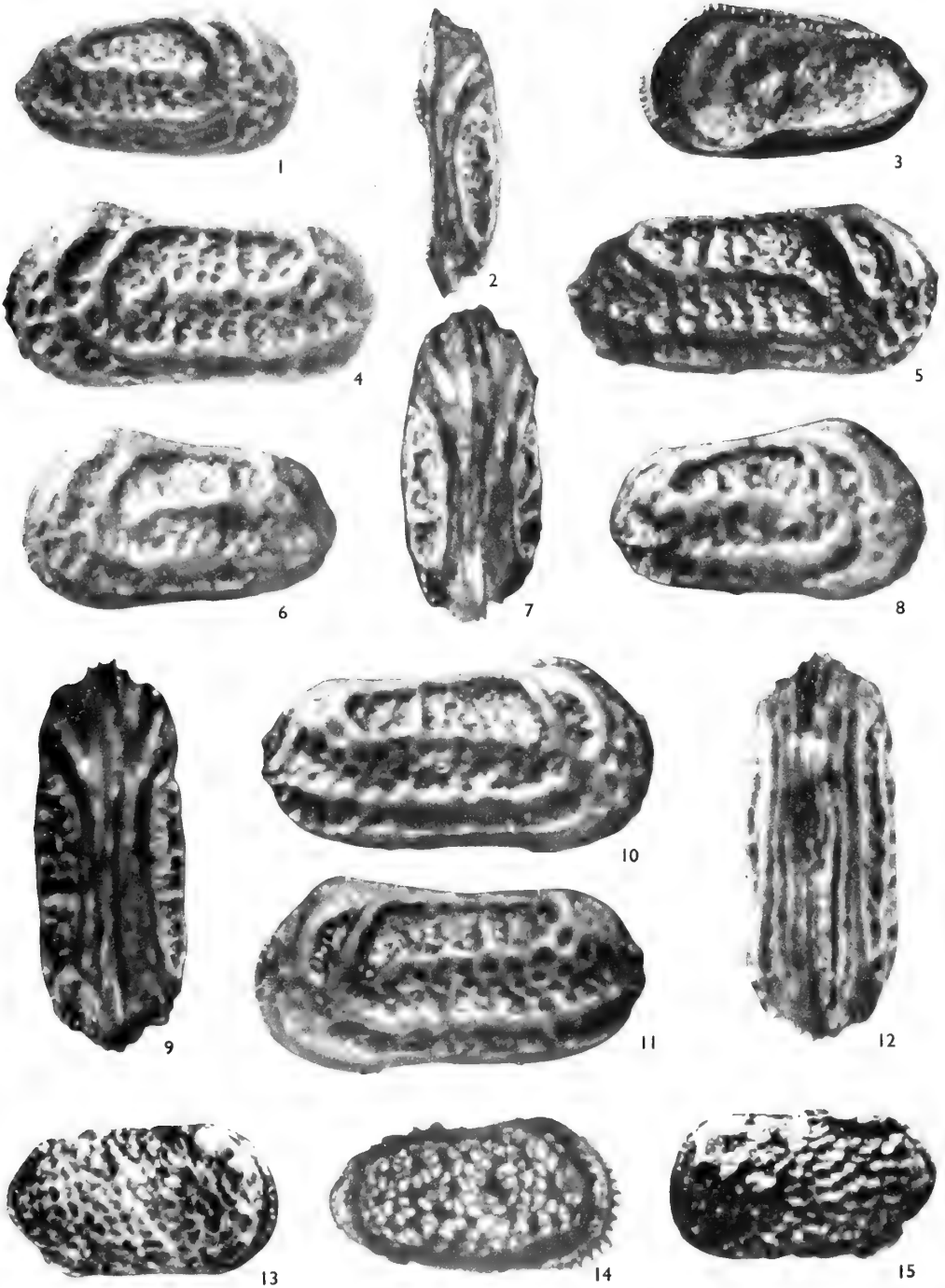
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PLATE 13

Fuhrbergiella (Praefuhrbergiella) horrida horrida Brand and Malz 1962 p.

FIGS. 1, 5. Female carapace (Io.5123) × 62
1. Dorsal view
2. Ventral view

FIGS. 2–4. Male right valve (Io.5124) × 62
2. External view
3. Internal view
4. Dorsal view

Palaeocytheridea parabakirovi Malz 1962 p.

FIGS. 6–9. Carapace (Io.5125) × 50
6. Right lateral view
7. Dorsal view
8. Ventral view
9. Left lateral view

Pleurocythere borealis borealis n. subsp. p.

FIGS. 10–13. Male right valve (HU.20.J.22), holotype × 58
10. External view in transmitted light
11. External view
12. Internal view
13. Dorsal view

FIG. 14. Male right valve (Io.5126), paratype × 58
14. External view

FIGS. 15, 17, 18. Female right valve (Io.5127), paratype × 58
15. Internal view
17. Dorsal view
18. External view

FIGS. 16, 19. Male right valve (Io.5129), paratype
16. Dorsal view
19. External view

FIG. 20. Male left valve (Io.5128), paratype
20. External view

FIGS. 21–24. Female carapace (Io.5130), paratype × 58
21. Right lateral view
22. Dorsal view
23. Ventral view
24. Left lateral view

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PLATE 14

Pleurocythere borealis carinata n. subsp. p

FIGS. 1, 2, 4. Female left valve (HU.20.J.28), holotype × 60
1. External view
2. Internal view
4. Dorsal view

FIGS. 3, 5, 7. Male left valve (Io.5131), paratype × 60
3. External view
5. Dorsal view
7. Internal view

FIGS. 6, 8, 11. Male right valve (Io. 5132), paratype × 60
6. Dorsal view
8. External view
11. Internal view

FIGS. 9, 10, 12, 14. Female carapace (Io.5133), paratype × 60
9. Dorsal view
10. Ventral view
12. Left lateral view
14. Right lateral view

Pleurocythere caledonia n. sp. p.

FIGS. 13, 15, 16, 18. Female left valve (HU.20.J.32), holotype × 57
13. Internal view in transmitted light
15. External view
16. Internal view
18. Dorsal view

FIG. 17. Female left valve (Io.5134), paratype × 57
17. External view

FIGS. 19, 21, 22. Male left valve (Io. 5135), paratype × 57
19. Dorsal view
21. External view
22. Internal view

FIGS. 20, 23, 24. Male right valve (Io.5136), paratype × 57
20. Dorsal view
23. External view
24. Internal view

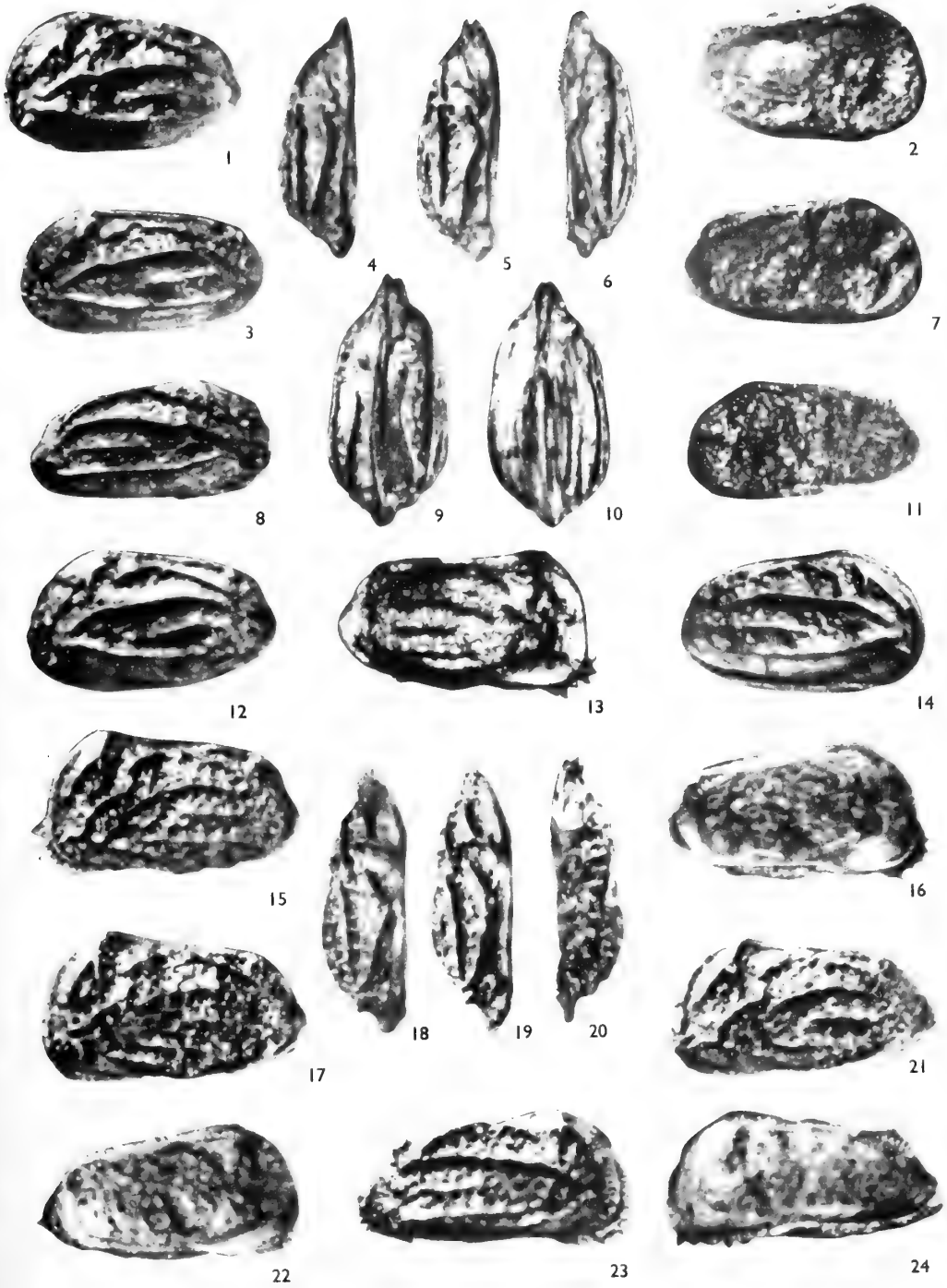
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PLATE 15

Pleurocythere caledonia n. sp. p.

FIG. 1. Female right valve (Io.5138), paratype × 57
1. External view

FIGS. 2–4, 11. Female carapace (Io. 5139), paratype × 57
2. Right lateral view
3. Left lateral view
4. Dorsal view
11. Ventral view

Pseudohutsonia hebridica n. sp. p.

FIGS. 5–7, 9. Female left valve (HU.20.J.66), holotype × 62
5. External view in transmitted light
6. Internal view
7. Dorsal view
9. External view

FIGS. 8, 14. Female right valve (Io.5141), paratype × 62
8. Dorsal view
14. Internal view

FIG. 10. Female left valve (Io.5140), paratype × 62
10. External view

FIGS. 12, 13, 16, 18. Female carapace (Io.5143), paratype × 62
12. Right lateral view
13. Left lateral view
16. Dorsal view
18. Ventral view

Pseudohutsonia sp. A. p.

FIGS. 15, 20, 21. Left valve (Io.5144) × 60
15. External view
20. Internal view
21. Dorsal view

Pseudoperissocytheridea parahieroglyphica n. sp. p.

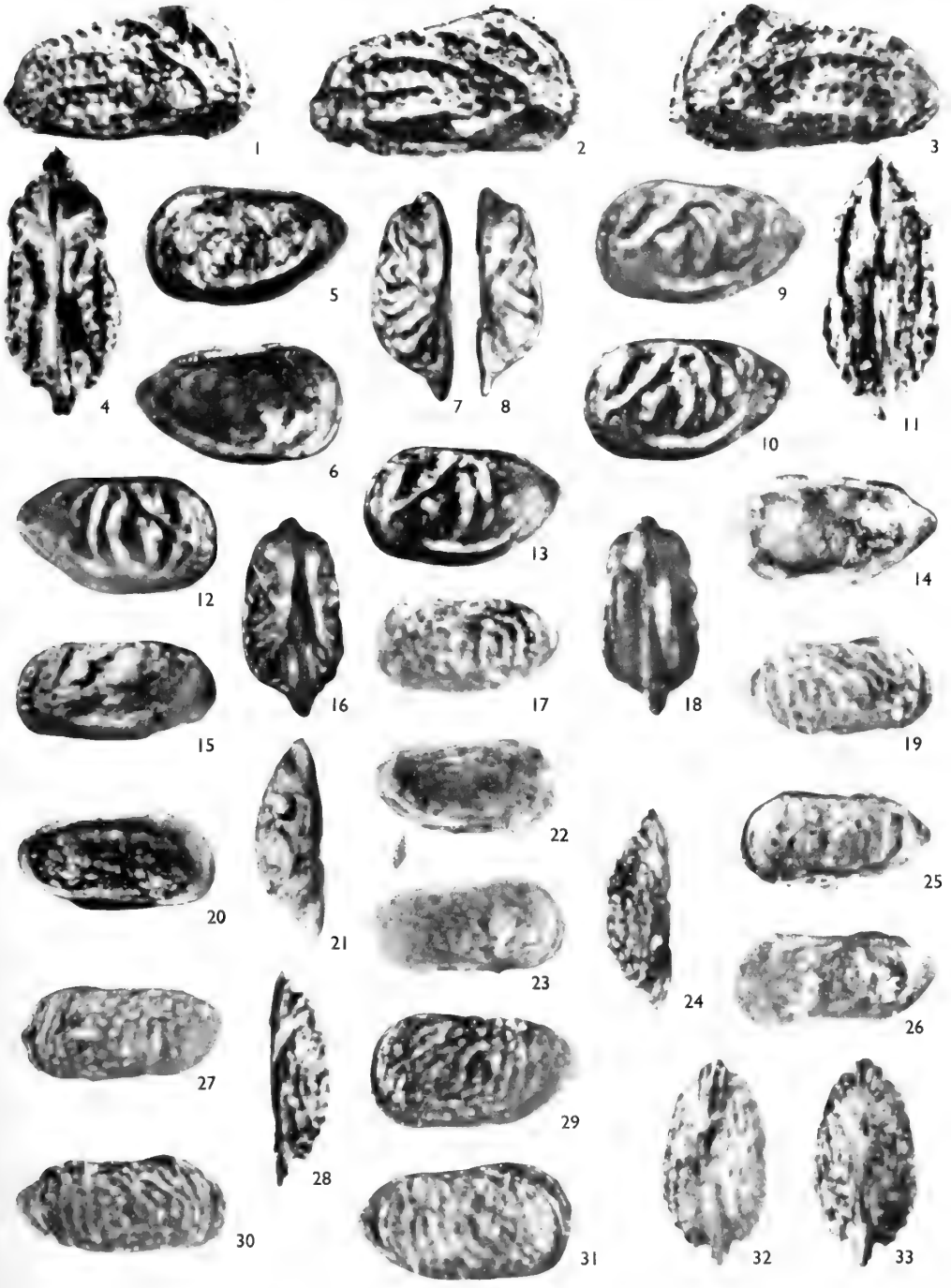
FIG. 17, 22. Female left valve (HU.20.J.13), holotype × 60
FIG. 17. External view
22. Internal view

FIGS. 19, 25. Female right valve (Io.5146), paratype × 60
19. External view
25. Internal view

FIGS. 23, 24, 27. Male left valve (Io.5147), paratype × 60
23. External view
24. Dorsal view
27. Internal view

FIGS. 26, 28, 30. Male right valve (Io.5148), paratype × 60
26. Internal view
28. Dorsal view
30. External view

FIGS. 29, 31–33. Female carapace (Io.5149), paratype × 60
29. Left lateral view
31. Right lateral view
32. Ventral view
33. Dorsal view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A PALYNOLOGICAL STUDY OF TWO OF THE NEOGENE PLANT BEDS IN DERBYSHIRE

M. C. BOULTER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 19 No. 7
LONDON: 1971

A PALYNOLOGICAL STUDY OF TWO OF THE NEOGENE PLANT BEDS IN DERBYSHIRE

BY

MICHAEL CHARLES BOULTER

Pp. 359–410 ; 9 *Plates*, 7 *Text-figures*

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World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.).

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Issued 15 *January*, 1971 *Price* £3.10

A PALYNOLOGICAL STUDY OF TWO OF THE NEOGENE PLANT BEDS IN DERBYSHIRE

By M. C. BOULTER

CONTENTS

		Page
I.	Introduction	362
II.	Classification and nomenclature	362
III.	Methods	366
IV.	Systematic part	367
	Sphagnaceae	369
	Lycopodiaceae	370
	Gleicheniaceae	371
	Osmundaceae	371
	Polypodiaceae	372
	Schizaeaceae ? / Polypodiaceae ?	373
	Taxodiaceae	374
	Pinaceae	375
	Podocarpaceae ?	379
	Papilionaceae ?	380
	Symplocaceae	381
	Nyssaceae	381
	Araliaceae	382
	Hamamelidaceae	383
	Salicaceae	384
	Myricaceae	384
	Betulaceae	385
	Fagaceae	386
	Corylaceae	387
	Juglandaceae	387
	Ulmaceae	388
	Aquifoliaceae	388
	Sapotaceae	389
	Ericaceae	390
	Onagraceae	390
	Compositae	391
	Liliaceae	391
	Graminae	392
V.	Quantitative analysis	392
VI.	Age determination	399
VII.	The Neogene environment in Derbyshire	402
VIII.	Acknowledgments	405
IX.	References	405

SYNOPSIS

Two of the sink hole deposits on the Derbyshire Carboniferous Limestone outcrop have been found to contain plant bearing clays. The pollen and spores that have been isolated from this

material are identified in terms of modern genera or form genera and species. Some of the 63 taxa which are described are shown, by comparison with fossil material from the continent of Europe, to be representative of Miocene and Pliocene deposits, and a Miocene/Pliocene boundary age is suggested for the assemblage. Quantitative pollen analysis from a vertical section through one of the deposits shows little variation in the floristic components, although there is a substantial change in the absolute concentration of palynomorphs. This suggests that the whole of the deposits, together with their contained pollen, may have been redeposited from a higher surface. Concordant with this concept is the separation within the assemblage of two floristic regions, one of heathland and the other of mixed woodland. The significance of the components of these floras is discussed in relation to plant distribution from the beginning of the Tertiary to the present day.

I. INTRODUCTION

A BRIEF description of some of the plant microfossils and macrofossils from two of the sink hole deposits (often called pocket deposits) in Derbyshire (Bee's Nest pit and Kenslow Top pit) have been given recently by Boulter & Chaloner (1970). While there is apparently no extempore geological method by which their age can be determined, palynological evidence does suggest a Neogene age, most probably Lower Pliocene. This age determination is of significance not only to the geomorphology of the whole deposits themselves, but also to Pennine uplift in general. What follows is an account of the pollen and spore assemblages found in these fossil plant bearing deposits. As it is the only study of Neogene palynology that has been made in the British Isles, its interpretation hinges largely on comparison with Continental assemblages of similar age.

There is a very large number of Neogene localities on the Continent of Europe which are of interest to the palynologist, though not all are of equal relevance to the Derbyshire assemblage. This is due not only to the regional variation of Neogene floras within Europe itself, producing what are often referred to as Facies Elements, but also to difficulties in correlation and palynological identification. Recently, some of the most crucial aspects of Neogene palynology, on a world-wide scale, have been concisely reviewed by Leopold (1970). Work from these centres has established the citation of palynological divisions within the Miocene and Pliocene ; no single continuous Neogene sequence is known however, and correlation between the several sites is not well understood. Particularly important to the present study is the discontinuity at the Miocene/Pliocene boundary, which makes this one of the least understood parts of the Neogene succession in Europe. Also, a recent revision of the radiometric time scale in the Cenozoic, based on foraminiferal zones (Berggren, 1969) suggests a far more recent dating (about $5\frac{1}{2}$ million years) of this boundary within the marine succession itself than was previously envisaged. The palynological divisions within the Neogene of The Netherlands and West Germany, shown in Figure 1, are of most relevance to the Derbyshire assemblage, though the correlation of these to the marine succession, and their chronostratigraphic extent, are both uncertain.

II. CLASSIFICATION AND NOMENCLATURE

The nomenclature of Neogene palynomorphs presents a difficult problem, which cannot be satisfactorily resolved for all the disciplines concerned. The same rules of

nomenclature that are used by neobotanists can be followed in Pleistocene palynology since the identification down to a living species is usually possible, whilst in Palaeozoic and Mesozoic work botanical affinities can rarely be concluded with confidence so that fossil form genera and species are incorporated into one or other system of morphographic classification. But the Neogene palynologist finds that his identifications fall within both of these categories. Some specimens can be

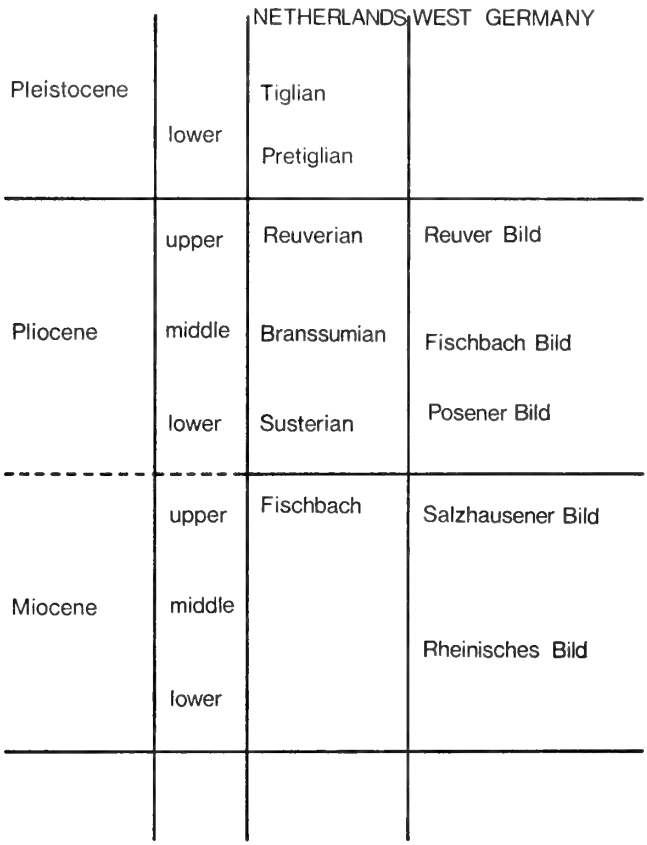

FIG. 1. Palynological divisions of the Neogene in The Netherlands and West Germany. The figure is not drawn to scale (see : Berggren, 1969), and the position of the Miocene / Pliocene boundary is only tentatively related to both series of divisions.

identified only as form genera and species, whilst others may be assigned to either modern genera or even to modern species. The resulting dissonance has been represented in many ways by different authors of Tertiary palynology (e.g. Thomson & Pflug, 1953 ; Traverse, 1955).

Normally, any Neogene palynomorphs that are encountered in European deposits can be assigned either to an extant genus or to a previously described form genus. And although some of the more recently created form species such as those of

Krutzsch (1962–1967) are delimited to a very narrow morphological range, earlier taxa such as those made by Potonié et al. (1950) and Thomson & Pflug (1953) are much more broadly circumscribed. So in the case of a commonly occurring Neogene palynomorph which cannot easily fit into a well defined form species or modern genus, use of the earlier more broadly defined form species can usually be made. All the palynomorphs that have been observed (in sufficient quantity—more than ten specimens) in the Derbyshire material, for instance, can either be attributed to a modern genus or else to a form genus with an established specific epithet. This practice must be interpreted most cautiously however, especially with regard to stratigraphic detail. Many of the taxa created by Thomson & Pflug, being of very broad circumscription, certainly represent more than one botanical species or even genus. Many have limited stratigraphic range and so are used as stratigraphic markers (Thomson & Pflug, 1953 ; von der Brelie, 1967). But since they are broadly circumscribed their known range is regularly extended as palynological work progresses, occasionally by forms slightly different from the type specimen but which none the less conform to the author's diagnosis. For example, in the Derbyshire assemblage, one pollen type is well described by a revised diagnosis for *Tricolpopollenites microhenrici* given by Thomson & Pflug (1953) ; some of their figures of this species are in agreement with the Derbyshire specimens too. But examination of their species from macerations of German browncoal show it to differ from the Derbyshire specimens in features not mentioned in the diagnosis (see page 386). Traditionally, this is sufficient reason for the creation of a new species, especially since *T. microhenrici* has been commonly regarded as a characteristic component of the European Miocene (von der Brelie, 1967). But the splitting of such broadly circumscribed form species into new taxa creates further problems. For instance, in the Derbyshire material alone, there are perhaps seven or eight slightly different pollen types which are all covered by Thomson & Pflug's diagnosis for *T. microhenrici*. The differences are indeed very slight, but they might be regarded as features warranting specific separation by a neopalynologist. Other European deposits have material assignable to this same form species which also shows a comparable range of variation. The creation of new species for each of these different types would produce quite an unworkable conglomeration of taxa ; it is unlikely that palynological techniques are sensitive enough to ensure adequate distinction, so they would have little practical significance either to the botanist or to the stratigrapher. Broadly based form taxa of the type adopted here avoid such confusion.

In such an instance as that mentioned above, a working solution has been proposed by Hughes and Moody-Stuart (1967). They suggest three grades of comparison, for a commonly occurring spore type, to the most appropriate published diagnosis, using a prefix cf. A, cf. B, cf. C. The type mentioned above would become " cf. C *T. microhenrici.* " The same authors have since suggested that these difficulties can be best overcome, when dealing with aspects of fine correlation, by abandoning the conventional Linnean system of nomenclature and substituting individual " biorecords " for specimens of separate assemblages (Hughes & Moody-Stuart, 1969). But since this present account primarily compares the Derbyshire assemblage with those previously described in Europe, this new and radical system

of palynological nomenclature is not directly relevant. For purposes of the present work no new taxa are created, and existing Neogene taxa are used and interpreted with caution, especially when comparing stratigraphic ranges.

An important factor to bear in mind in this context of describing palynological taxa is the future role of the scanning electron microscope. It is likely that when these instruments become generally available to the palynological world they will encourage a more accurate and reliable specific diagnosis for both extant and fossil material. In the interim therefore, this gives further reason to reduce the formation of new taxa to an absolute minimum.

In describing this Derbyshire assemblage then, no palynomorphs have been identified as an extant genus together with either an extant or fossil specific epithet. Such names have often been used in the Tertiary however, for instance by Macko (1957) and Traverse (1955) respectively. It is hazardous enough to assign Tertiary pollen and spores to a modern genus ; this view is evidently held by many workers using form taxa right up to the Pleistocene. Assuming that many modern species did exist in say the European Miocene, it is unlikely that the characters defining all their pollen and spores are distinctive enough to allow separation at the specific level. Reference material of all modern species of the genera which are known from macrofossils to have occurred in the European Tertiary is not available to many palynologists ; and if it were it is unlikely that light microscope techniques are accurate enough to ensure uncontroversial identification of each species. But the premise, that modern species did exist in the European Miocene, is unacceptable to many. The macrofossil record (see for example Němejc, 1968, and *in press*) suggests that few modern species were present in the whole of the European Tertiary. There seems to be little justification therefore to identify Neogene palynomorphs in terms of extant species of extant genera. In assigning fossil species to modern genera, Traverse (1955) made the assumption that gametophytic characters in angiosperm and gymnosperm genera can be used as a basis for erecting new plant species names in the same way as plant taxonomists use the sporophyte characters of modern plants. The method seems to have been adopted rarely in Europe, and so need not be further considered in the context of comparing members of the Derbyshire assemblage with their geographical neighbours.

Most systems of classification for fossil spores and pollen are purely morphographic, with no reference to the botanical affinities of the organisms concerned. That of Thomson & Pflug (1953) for instance, was established with the view of incorporating Neogene material just as well as forms from the Mesozoic or Palaeozoic. Few authors of Neogene palynology have ever used these systems, though there are some exceptions for Miocene work (e.g. Mazancova, 1962). Two other morphographic systems are of special interest to Tertiary workers. Van der Hammen's (1956) is based on taxa typified in terms of the spores or pollen of extant species. For example, he typifies the form genus *Monocolpites* on the type specimen *Orthrosanthus chimboracensis* (Iridaceae). Monocotyledon pollen then is the type material for a genus which is also used for fossil gymnosperm pollen e.g. *Sciadopitys*. Another system adopted by Krutzsch (1957) and later by Sonntag (1966) created 125 morphological units termed form-groups, selected for their stratigraphic unity within the Tertiary.

The components of each group are quite diverse, especially botanically, though systematic subdivision of each group has not been attempted.

Since, in the European Neogene, it is possible to relate nearly all pollen and spores to a botanical family, the Neogene/Paleogene boundary may be taken as the level above which the purely morphographic system can be replaced with some system based on botanical systematics. In order to include those forms which cannot be assigned reliably to a family, as is the case with some form species, they are either placed in " *Incertae Sedis* " (Traverse, 1955 ; Rouse, 1957 ; Pons, 1964 ; Couper, 1953) or else the most eligible family is shown as a heading preceded by a question mark (Potonié et al., 1950 ; Doktorowicz-Hrebnicka, 1957 ; Pacltova, 1963). For purposes of continuity within the systematic part of this paper, this latter method will be adopted here, subdivided by both form genera and species, or else by modern genera alone.

Several difficulties with this system do arise however. Some Neogene form species cannot be assigned (from comparison of the fossil type with Recent material) with certainty to any botanical family. For instance in the case of *Tricolpopollenites ipilensis* Pacltova, a similar pollen type is found in modern members of both the Leguminosae and the Salicaceae. In the system of classification used here, the question marks are very important. But it is hoped that the resulting layout is conformable with the International Code, and will avoid the problems that occur in systems which have a morphographic " addenda " or which incorporate the botanical affinity in the form generic name (Rouse, 1957).

Another difficulty arises from different opinions concerning the role of the form-species : some have advocated recognition of large broadly defined units, while others favour small ones with very precise diagnoses. These two opposing views are supported by, among others, Skarby and Krutzsch respectively. Krutzsch's method of morphological description involves very accurate measurement so creating large numbers of new taxa, whilst Skarby's species have synonomy with many taxa of other authors and cover wide stratigraphic ranges. *Gleicheniidites senonicus* Ross, as emended by Skarby (1964) extends from Jurassic to Pliocene deposits and has synonomy with 37 previously cited taxa. Both extremes however are able to convey accurate information : at the risk of being considered hypocritical, I adopt both practices in the systematic part of this paper.

Arguments in response to the present high output of new taxa are well known. On the one hand (Hughes & Moody-Stuart, 1967) we are advised to consolidate within the present taxa, so that few more new species need be made, at least by the Linnean system. Whilst on the other hand (Faegri et al., 1967), encouragement is given to " propose new artificial taxa " in " cases of uncertain identification . . . involving loose or inexact " comparison. It is hoped that this paper will show that this latter view is not necessarily applicable to European Neogene palynology, at least.

III. METHODS

Pollen preparations have been made by macerating 1 c.c. samples of plant bearing clay in hydrofluoric acid in the cold, for up to four hours. The residue was shaken in

10% hydrochloric acid, centrifuged, and the sediment then floated in zinc bromide solution (specific gravity 1·9). Especial care was taken in the preparation of the series of macerations used to determine the Absolute Pollen Frequency (see Section 5). Equal weights to the nearest milligram of air dried sample were macerated, each in precisely the same way, with the addition of equal volumes of reagents to each sample. To ensure that an equal volume of suspension was evenly distributed under the coverslip of each preparation, the pollen counts were checked by the use of a haemocytometer.

The preparations of all the palynomorphs figured in this paper are deposited in the British Museum (Natural History), together with a representative range of clay samples. Although the Derbyshire exposures referred to in Section V are exposed at the date of going to press, plans of the Bee's Nest pit owners are underway to remove the plant bearing bed in the near future.

A reference collection has been prepared of pollen and spores from Recent species of most of the genera mentioned in Section IV. Many authors (Traverse, 1955 ; Faegri & Iversen, 1964) stress the importance of such a collection to those engaged in Tertiary palynology, especially as an aid to identification. But since there is great variation in pollen morphology within most genera found in the Derbyshire flora, the collection was found to be of little use in identification beyond the generic level. Of comparable value to this modern pollen reference collection is the comparative reference material from Neogene deposits of West Germany, East Germany and Czechoslovakia. When used in conjunction with the published descriptions of the deposits concerned, such comparison was found to be of great value for purposes of identification. The view is presented in Section VI that in the Lower Pliocene of Europe, the vegetation is likely to have been made up of very few species that frequent Europe today. So to obtain full benefit from Recent comparative material it is necessary to refer to pollen from every living species of each genus—a very exacting task.

IV. SYSTEMATIC PART

Each of the 63 taxa which have been identified from the Derbyshire material (listed in Table 1) are discussed in this section. They are arranged under the heading of their botanical family, and where this is in doubt, the family name is followed by a question mark.

Table 1

List of the pollen and spore taxa which have been identified within the Derbyshire assemblage.

SPHAGNACEAE

1. *Stereisporites* (*Stereisporites*) *minor microstereis* Kr.
2. *S.* (*Stereisp.*) *stereoides stereoides* (R. Pot. & Ven.) Th. & Pf.
3. *S.* (*Distancoraesporis*) *crucis* Kr.
4. *S.* (*Distanc.*) *wehningensis* Kr.
5. *S.* (*Distanc.*) *germanicus rhenanus* Kr.
6. *S.* (*Distverrusporis*) *pliocenicus pliocenicus* Kr.

	7. *S.* (*Distgranisporis*) *minimoides* Kr.
	8. *S.* (*Distgran.*) *granisteroides* Kr.
	9. *S.* (*Stereigranisporis*) *semigranulus* Kr.
	10. *S.* (*Stereigran.*) *magnoides* Kr.
	11. *S.* (*Distzonosporis*) *microzonales* Kr.
LYCOPODIACEAE	12. *Lycopodium* sp.
GLEICHENIACEAE	13. *Gleicheniidites senonicus* Ross, emended Skarby
OSMUNDACEAE	14. *Osmunda* sp.
POLYPODIACEAE	15. *Laevigatosporites haardti* (R. Pot. & Ven.) Th. & Pf.
	16. *Verrucatosporites favus* (R. Pot.) Th. & Pf.
SCHIZAEACEAE ?/	17. *Leiotriletes wolffi wolffi* Kr.
POLYPODIACEAE ?	18. *L. wolffi brevis* Kr.
	19. *Triplanosporites microsinuosus* Pf.
TAXODIACEAE	20. *Inaperturopollenites hiatus* (R. Pot.) Th. & Pf.
	21. *I. dubius* (R. Pot.) Th. & Pf.
	22. *Cryptomeria* sp.
	23. *Sciadopitys* sp.
PINACEAE	24. *Abies* sp.
	25. *Cedrus* sp.
	26. *Keteleeria* sp.
	27. *Picea* sp.
	28. *Pinus* sylvestris-type
	29. *P.* haploxylon-type
	30. *Tsuga* canadensis-type
	31. *T.* diversifolia-type
PODOCARPACEAE ?	32. *Podocarpoidites libellus* R. Pot.
PAPILIONACEAE ?	33. *Tricolpopollenites ipilensis* Paclt.
	34. *T. liblarensis fallax* (R. Pot.) Th. & Pf.
	35. *T. liblarensis liblarensis* (Th.) Th. & Pf.
SYMPLOCACEAE	36. *Porocolpopollenites rotundus* (R. Pot.) Th. & Pf.
	37. *P. vestibulum* (R. Pot.) Th. & Pf.
NYSSACEAE	38. *Nyssa* sp.
ARALIACEAE	39. *Hedera* sp.
	40. *Tricolporopollenites edmundi* (R. Pot.) Th. & Pf.
HAMAMELIDACEAE	41. *Liquidambar* sp.
SALICACEAE	42. *Salix* sp.
	43. *Tricolpopollenites retiformis* (R. Pot.) Th. & Pf.
MYRICACEAE	44. *Myrica* sp.
BETULACEAE	45. *Alnus* sp.
	46. *Trivestibulopollenites betuloides* Th. & Pf.
FAGACEAE	47. *Tricolpopollenites microhenrici* (R. Pot.) Th. & Pf.
CORYLACEAE	48. *Corylus* sp.
	49. *Carpinus* sp.
JUGLANDACEAE	50. *Juglans* sp.
	51. *Carya* sp.

ULMACEAE	52. *Ulmus* sp.
AQUIFOLIACEAE	53. *Tricolporopollenites iliacus* (R. Pot.) Th. & Pf.
	54. *T. margaritatus* (R. Pot.) Th. & Pf.
SAPOTACEAE	55. *Tetracolporopollenites sapotoides* Th. & Pf.
ERICACEAE	56. *Empetrum* sp.
	57. *Calluna* sp.
	58. *Erica* sp. ?
	59. *Rhododendron* sp. ?
ONAGRACEAE	60. *Corsinipollenites maii* Kr.
COMPOSITAE	61. *Compositoipollenites rizophorus* R. Pot.
LILIACEAE	62. *Periporopollenites echinatus* (Wode.) Th. & Pf.
GRAMINAE	63. *Graminidites media* Cookson.

SPHAGNACEAE

1. *Stereisporites* (*Stereisporites*) *minor microstereis* Kr.
2. *S.* (*St.*) *stereioides stereoides* (R. Pot. & Ven.) Th. & Pf.
3. *S.* (*Distancoraesporis*) *crucis* Kr.
4. *S.* (*Distanc.*) *wehningensis* Kr.
5. *S.* (*Distanc.*) *germanicus rhenanus* Kr.
6. *S.* (*Distverrusporis*) *pliocenicus pliocenicus* Kr.
7. *S.* (*Distgranisporis*) *minimoides* Kr.
8. *S.* (*Distgran.*) *granisteroides* Kr.
9. *S.* (*Stereigranisporis*) *semigranulus* Kr.
10. *S.* (*Stereigran.*) *magnoides* Kr.
11. *S.* (*Distzonosporis*) *microzonales* Kr.

(Pl. 1, Figs. 1–11)

Spores assigned to this family are very commonly found throughout the whole European Tertiary. Many authors are in the habit of assigning them to *Sphagnum* sp. despite the lack of any supporting evidence from macrofossils that this genus commonly existed in the Tertiary. The spores are indeed comparable with those of the extant genus but it is hard to prove specific identity with any of the present British species (Tallis, 1962). The only Tertiary macrofossil remains from Europe, though without spores *in situ*, are described from the Miocene of Willershausen (Straus, 1952) and Upper Silesia (Szafer, 1961), and these do not compare closely with any living species.

Krutzsch's Atlas (1963b) describes no fewer than 64 form species of the form genus *Stereisporites*, which he regards as having affinity with the modern genus *Sphagnum*. The form genus was originally diagnosed by Thomson and Pflug (1953) who recognized three form species, though Potonié and Venitz (1934) described *Sporites stereoides* which remains the type species of the new form genus. Krutzsch divides the taxon into seven form sub-genera on the basis of the type of distal differentiation, the presence of granulate sculpturing, and the presence of a cingulum. By their very

nature as artificial form species, and on occasions as form sub-species, there can be no reliable estimate of the number of once living species that they represent.

The spore walls of the Sphagnaceae seem to have rather unusual properties. In Recent material the mature spores take up safrannin stain less effectively than immature ones. In fossil material they seem to be less well preserved than other spore types. Severe maceration has also been found to effect them more than most vascular plant spores, it often having the effect of changing the morphological characteristics to produce a spore which is immediately recognizable as one which has been so treated. Within the eleven species identified from the Derbyshire material, six form sub-genera are represented ; controversial identification is thereby reduced.

In his Atlas, Krutzsch cites a " stratum typicum " for each form species : those found in the Derbyshire assemblage fit this intimation of age very well. This however, does not mean that Krutzsch's stratigraphic observations are to be regarded as the concise ranges for each type. Other authors have attached no such significance to the use of spores from this family as stratigraphic markers, the range of the family in Europe being from the Jurassic to the present.

LYCOPODIACEAE

12. *Lycopodium* sp.

(Pl. 2, Fig. 1)

Apart from variation in the shape in outline from round to triangular, there seems to be complete morphological uniformity in all the *Lycopodium* specimens found in both Derbyshire localities. Examination of spore macerations of the modern species *L. clavatum* show a similar variation in shape. The species found here differs from this modern British species in having fewer, though larger, reticulum meshes.

Since there has been just one species found here, and since the morphology of *Lycopodium* spores seems to be distinctive for the genus, the extant generic name is used. *Reticulatisporites* (Ibrahim, 1933 emend. Pot. & Kr., 1955) includes many species with reticulum meshes of larger size than the extant European species of *Lycopodium*, in the same way as the Derbyshire specimens ; but in the Tertiary, this form genus is usually assigned to *Lycopodium* sp.

Krutzsch (1963, a) gives a comprehensive review of twenty nine form genera which can be assigned to the Lycopods, whilst making new combinations for all lycopodiaceous spores to *Retitriletes* (van der Hammen, 1956, emend. Krutzsch, 1963, a), *Camarozonosporites* (Pant, ex. Pot. 1956), or *Selagosporis* (Krutzsch, 1963, a). The Derbyshire species closely resembles *Retitriletes rueterbergensis* (Krutzsch, 1963, a), and also a figured specimen which Mazancova (1962) refers to *Reticulatisporites potoniei* Th. & Pf., though these two taxa are not synonymous. This particular conflict demonstrates the confusion that has been caused by the creation of so many taxa for this family ; it is most likely that many species have been based on features of preservation.

GLEICHENIACEAE

13. *Gleicheniidites senonicus* Ross, emended Skarby

(Pl. 2, Fig. 2)

The recognition of spores from this family is both a complex and controversial matter, mainly as a result of difficulties in interpreting the three dimensional spore morphology as seen by the light microscope. Bolchovitina (1967) proposed the use of four form-genera within the Gleicheniaceae, each differing in characters of the equatorial thickening, corner projections, or sculpturing. The Derbyshire specimens are assignable to one of these form-genera, *Gleicheniidites* (Ross, 1949) as *G. senonicus*, the type species having been recently revised by Skarby (1964).

The Derbyshire spores, as well as other gleichenioid types described by Thomson and Pflug (1953) and Krutzsch (1959) often show a feature that has been referred to as a " torus " ; indeed, Krutzsch makes use of variation in this feature when separating new sub-form-genera within *Gleicheniidites*. Skarby however points out that the structures described by these authors are not tori in a morphological sense, but rather phenomena resulting from optical sections of the inwardly curving wall. Skarby's conclusion is that the outer part of the wall of *G. senonicus* is completely smooth, and she has made comparable observations of this from material of Krutzsch's *Neogenisporis neogenicus* and Thomson and Pflug's *Concavisporites acutus, C. argulatus* and *C. obtusanglus*. All these form-species she has placed in synonomy with *Gleicheniidites senonicus*, and this is accepted here.

There is great range in both the size and shape of the " torus " in the specimens of *G. senonicus* which have been examined from Derbyshire, and often it is completely absent. This variation could be due to the spore's orientation, or even to the degree of compression.

Thomson and Pflug (1953) and Krutzsch (1959) both stress that their gleichenioid spores are important Mesozoic—Lower Tertiary index fossils. Krutzsch however, has described two occurences of spores, now assigned to *G. senonicus*, from the Neogene. One is from the Miocene at Leipisch (*Neogenisporis neogenicus* Kr. 1962) and the other from the Pliocene at Rüterberg (originally *Cingulatisporites pseudoneddeni* Kr. 1959 ; then included in *N. neogenicus* Kr. 1962). This Derbyshire record gives support to Skarby's claim that *G. senonicus* ranges in Europe from the Jurassic to the Pliocene. Though the modern species of the family now occupy mainly tropical environments, a few species do occur in the southern temperate zone of Europe. If the Pliocene plant was at all similar to those of the modern genera of the family, the climate in Pliocene Derbyshire must have been frost-free.

OSMUNDACEAE

14. *Osmunda* sp.

(Pl. 2, Fig. 3)

Spores from this family have been referred to the modern species more readily than most other pollen and spore types found in the Neogene. Zagwijn (1960) and Pons

(1964) for instance both distinguish between *Osmunda regalis* and *O. claytoniana* : the latter having been previously described from the Polish Pliocene (Szafer 1954). Comparisons of fossil specimens have also been made to the extant *O. javanica* and *O. regalis* by Leschik (1951) and also Neuy-Stolz (1958). Morphological similarities led Leschik to set up *O.* regloide-type and *O.* javonicoide-type, though only the latter closely resembled the modern equivalent in size range.

Two form-genera, *Rugulatisporites* Th. & Pf., and *Baculatisporites* Th. & Pf. have been applied to spores from this family, though the latter has been compared by the original authors to *Pteridium* spores. *Rugulatisporites* was originally diagnosed as having elongate sculpturing elements, whilst *Baculatisporites* is baculate. Krutzsch (1967) however has referred the Thomson and Pflug type species for *Rugulatisporites* to the new combination *Baculatisporis quintus* which is based on the genotype *B. primarius* (Wolff, 1934) Th. & Pf.

Due to the absence of really well preserved specimens, it is not possible to assign the Derbyshire specimens to any of these form taxa.

POLYPODIACEAE

15. *Laevigatosporites haardti* (R. Pot. & Ven, 1934) Th. & Pf. 1953
16. *Verrucatosporites favus* (R. Pot., 1931) Th. & Pf. 1953

(Pl. 2, Figs. 4–6)

Laevigatosporites is the form-generic name originally proposed for smooth walled bilaterally symmetrical monolete spores, occurring from the Carboniferous to the Tertiary. Potonié (1967) assigns the form genus to Palaeozoic Sphenophyllaceae and Calamitaceae, whilst other authors accept that the Tertiary forms of the genus are from plants of the Polypodiaceae. Krutzsch (1967) divided the species into three form sub-species, differing mainly in size and shape, though all have Miocene "*stratum typicum*". *L. haardti haardti* Krutzsch is by far the most widely occurring of the three groups, and most closely resembles the Derbyshire specimens. It is found commonly in most Tertiary deposits of Europe ; Krutzsch lists many of the European Neogene occurrences in his list of synonomies.

The form genus *Verrucatosporites* was set up by Thomson and Pflug (1953) with a Tertiary type species. Potonié's original species *Polypodiisporites favus* (combined by Thomson & Pflug into *V. favus*) has been separated into four subform species by Krutzsch (1967) again mainly on differing size characters. Though perhaps commonest in the European Miocene, the species has no stratigraphic significance other than a broad Tertiary occurrence. The species closely resembles *Polypodium vulgare* which is now very widely distributed within the British Isles. This modern specific name has been used by some authors (e.g. Zagwijn, 1960) to describe Pliocene material.

SCHIZAEACEAE ? or POLYPODIACEAE ?

17. *Leiotriletes wolffi wolffi* Kr.
18. *L. wolffi brevis* Kr.
19. *Triplanosporites microsinuosus* Pflanzl

(Pl. 2, Figs. 7–9)

The two subspecies of *Leiotriletes wolffi* set up by Krutzsch (1962) fit precisely two spore types occasionally found in the Derbyshire assemblage. Krutzsch describes specimens of both form-subspecies from the German Miocene and Pliocene, but avoids relating them to any botanical family. Comparison with spores from modern *Lygodium* and *Pteridium* species shows similarity to both fossil types, but little to distinguish one genus from the other. Confirming these observations, Thomson & Pflug (1953) suggest affinity to both these extant genera for their Tertiary species of the form-genus *Laevigatisporites* which Krutzsch has combined into the form-genus *Leiotriletes*, adding to it several completely new species which occur in the Miocene and Pliocene. Both smooth walled schizaeaceous spores and the indistinguishable polypodiaceous types have been referred to other form-genera, such as *Lygodiumsporites* (R. Pot. & Gell., 1933) emend. R. Pot. 1956, and *Toroisporitis* Krutzsch, 1959. In his monograph on spores of the genus *Schizaea*, Selling (1944) shows morphological types including the smooth walled and rugulate monolete forms, little different to those commonly assigned to *Polypodium* sp.

Apart from rather dubious records of *Lygodium* from the Pliocene of southern France (Pons, 1964), and *Schizaea* cf. *pusilla* (see Potonié, 1967) from the Pliocene of Rüterberg (Krutzsch, 1959), Krutzsch's (1962) records of *Leiotriletes wolffi* and *Toroisporitis* ? *pliocaenicus* are the only other specimens of this *Lygodium*-like spore to have been described from strata more recent than the Miocene in Europe. Krutzsch (1957) himself previously recognized spores of this kind (form groups 13, 14 and 15) from the Cretaceous up only to the middle Miocene. The macrofossil record gives no evidence of any Schizaeacous genus being present in Europe later than the record from the Lower Miocene of Germany by Kräusel & Weyland (see Gothan & Weyland, 1964, p. 203). In the Dorset and Hampshire Paleocene, Chandler (1955) described fertile material with spores of this type from species of *Aneimia* and *Lygodium* ; but five genera of the Polypodiaceae were present as macrofossils in the Bournemouth Beds. This family occurs again in Britain in the Ludham borehole (= Tiglian) as *Pteridium aquilinum* (West, 1961). The Derbyshire record then, could either represent an intermediate of the Polypodiaceae (*Pteridium*) record through the Tertiary into the Pleistocene, or else mark one of the last occurrences of *Lygodium* in Europe.

Grebe (1953) has suggested that *Lygodium* is a pioneer plant following forest fire. In the Miocene German browncoals the spores of the genus are most commonly found on top of fusinite layers of coal, itself a product of such fires. Some of the macrofossil material found in the Bee's Nest pit has a type of preservation which suggests that forest fires occurred in Derbyshire during the formation of the deposit.

Triplanosporites microsinuosus Pflanzl is shown by Krutzsch (1967) to occur from the Oligocene to the Pliocene in Germany. Potonié (1967) suggests that this whole

form-genus might be assigned to either the Schizaeaceae or else to the Dipteridaceae or Dicksoniaceae.

TAXODIACEAE

20. *Inaperturopollenites hiatus* (R. Pot.) Th. & Pf.
21. *I. dubius* (R. Pot.) Th. & Pf.
22. *Cryptomeria* sp.
23. *Sciadopitys* sp.

(Pl. 3, Figs. 1–4)

Previous authors of works on Tertiary palynology have described pollen of the Taxodiaceae (exclusive of *Sciadopitys*), in one of three ways. Doktorowicz-Hrebnicka (1959) and Oszast (1960) explain features which make it possible to distinguish Neogene papillate pollen at the generic level, though implying that broken or gaping taxodiaceous pollen is not identifiable in this way. Zagwijn (1960) used just two groups, *Taxodium*-type (cf. *Taxodium* and *Glyptostrobus*) and *Sequoia*-type (cf. *Sequoia*, *Cryptomeria* and *Metasequoia*) with small and large papillae respectively. He made no further distinction at the generic level, and included all gaping forms without papillae in the group Varia. Pons (1964) adopted these same two divisions, but made tentative suggestions at generic identification within each group. Other authors approve of the advice given by Potonié (1967) that separation of taxodiaceous (excluding *Sciadopitys*) pollen is not at all reliable at the modern generic level ; consequently, the use of form taxa is preferable to the use of modern generic names.

Of these controversial taxodiaceous forms, three types occur in the Derbyshire assemblage. They are all present in very low frequencies, in contrast to the situation in the majority of West European Pliocene deposits where they form a major component of the pollen assemblages. Specimens of papillate forms occur, though very rarely, and are assigned to *Cryptomeria* sp. on account of their long curved papilla—a character of pollen from this genus mentioned by Doktorowitz-Hrebnicka. The occurrence of macrofossil *Cryptomeria* in the same Derbyshire deposit gives further support to this identification (Boulter, *in press*). Two forms of gaping taxodiaceous pollen also occur, but the papillae are never visible. Examination of modern material shows that the pollen grains begin to split open along the axis of the papilla, so that when gaping fully open, the papilla is quite unrecognizable. *Inaperturopollenities dubius* is a form species for one such gaping type. It has a relatively thin exine, not exceeding 0·5 μ in thickness, and often has secondary folds. The exine is very finely intrapunctate, and the grain is always oval in shape. Spores of modern *Equisetum* are very similar to this form, but since no elators have been found in any of the preparations, the possibility of its occurrence is felt to be remote. *Inaperturopollenites hiatus* has a thicker (more than 0·5 μ) smooth exine, and is always spherical in outline.

Sciadopitys pollen is mococolpate and coarsly verrucate, quite distinctive enough to make the form name *Monocolpopollenites serratus* (R. Pot. & Ven.) Th. & Pf. unnecessary in this case, especially since there are macrofossil remains of *Sciadopitys*

tertiaria leaves in the same Derbyshire deposit. Although *Sciadopitys* pollen has been recorded as high as the Tiglian, it is rarely so abundant as in this assemblage. Only at a few sites (von der Brelie, 1959, p. 34) does it exceed 10% of the total pollen count, the genus having gradually diminished in significance since the time of deposition of the *Sciadopitys* Graskohle during the Miocene.

PINACEAE

24. *Abies* sp.
25. *Cedrus* sp.
26. *Keteleeria* sp.
27. *Picea* sp.
28. *Pinus* sylvestris-type
29. *P.* haploxylon-type
30. *Tsuga* canadensis-type
31. *T.* diversifolia-type

Abies sp.

(Pl. 3, Fig. 5)

This pollen has been differentiated from that of *Keteleeria* occurring in this assemblage by reference to the thickness of the exine at the proximal face of the corpus. In specimens of *Abies*, this measures about 10 μ, whilst the corpus of *Keteleeria* pollen has proximal exine no thicker than 4 μ. The sculpturing elements are so similar that they have not been used to separate the pollen from the two genera. Indeed, Zagwijn (1960) did not separate them at all, whilst others who have done so rarely give full justification, as explained by Ferguson (1967, p. 85).

The genus has been commonly reported from more than one of the British interglacials, though specific identification has not proved possible. However, the genus was not identified from either the Ludham borehole (= Tiglian) or from any of the investigations on the lower Tertiary floras of southern England. Its occurrence in Derbyshire, both as pollen and leaf material, is the sole record of the genus in the whole of the British Tertiary, though it was extremely widespread on the continent of Europe during this time.

Cedrus sp.

(Pl. 3, Fig. 6)

The sacci of these pollen grains are usually in the contracted position, but the pollen is best identified by the marginal crest on the proximal part of the sacci, which continue onto the edge of the corpus. Despite its absence in the British Pleistocene, the occurrence of the genus in the Derbyshire Pliocene is not surprising. Its pollen has previously been found in the lower Tertiary deposits of southern England (Pallot, 1961) and Scotland (Simpson, 1961) whilst on the European continent, Neogene and Pleistocene records trace its restriction into present day northern Africa and the Middle East. This migration is well shown in a series of maps reproduced by

Ferguson (1967). The present record marks its most northerly known occurrence since the Paleogene, due no doubt, to the high oceanicity of the climate in west Europe, a factor which is evidently still important in the distribution of *Cedrus lebani*. Comparable Pliocene records are made by Potonié et al. (1950) from Wallensen, and its occurrence in the same area is recorded by Kremp (1950) from the browncoals. The form found at Wallensen has been described by Thomson & Pflug (1953) as *Pityosporites cedroides*, a name used since by Mazancova (1962) for her Miocene material from Bohemia. This is indistinguishable from the Derbyshire specimens.

Keteleeria sp.

(Pl. 3, Fig. 7)

Not only is the pollen of this genus difficult to identify, but the macrofossil remains can be easily confused with those from other members of the family. So all parts of the fossil record of *Keteleeria* must be interpreted critically. Ferguson (1967) suggested that only four published records of *Keteleeria* pollen from the whole European Tertiary are authentic ; three are from the Miocene and one from the Eocene. Pollen is convincingly recorded in the Pliocene too however, by Pacltova (1963) from southern Bohemia, and by Zert (unpublished thesis, 1960) from N.E. Bohemia.

Picea sp.

(Pl. 4, Fig. 1)

The sculpturing on both sacci and corpus of these pollen grains is finer than in any other extant bisaccate genus; there are no marginal crests to the saccus ornamentation, whilst in lateral longitudinal view, the edge of the sacci form a smooth curve with the edge of the corpus. The longest axis is 70–90 μ.

Both macrofossils and pollen from the genus have been commonly found in the European Tertiary and Pleistocene. In the Neogene, where Thomson & Pflug's name *Pityosporites alatus* is rarely used, there are many instances of more than one species of *Picea*. In the German Miocene, Potonié et al. (1950) illustrate a *Picea* pollen as well as a smaller " *Picea* omorikoide-type ". In the Pliocene, Pons (1964) makes comparisons of three different types with living species, whilst Zagwijn (1960) distinguished between a large form corresponding to *Pityosporites alatus* and a smaller one about the size of *Pinus* pollen. A smaller type may also occur in the Derbyshire material, though its rare occurrence and similarity, especially in polar view, to *Pinus* haploxylon-type makes it very difficult to recognise. Manum (1962) found similar difficulty in dealing with the Lower Tertiary pollen that he refers to as *Abietineae-pollenites* sp. Type A. It has, he says, affinity with either *Pinus* or *Picea*, and especially to *Pityosporites microalatus* f. *major* (R. Pot.) Th. & Pf.

Pinus haploxylon-type
Pinus sylvestris-type

(Pl. 4, Figs. 2–3 ; Pl. 5, Figs. 1–5)

Both these names are used in the sense that they have unknown affinity to any living species of the genus. It is unfortunate that *Haploxylon* is one of the two subdivisions of the genus *Pinus* (see Mirov, 1967) and that the only living species indigenous to the British Isles is *P. sylvestris*. Both names were originally used with just such comparative implications, but reference to pollen from living material shows that the synonomy is very insecure. For instance, Pons (1964) compared both types to pollen from several modern species but was unable to make direct synonomy. The terminology was introduced by Rudolph (1935), in one of the first major studies of European Tertiary palynology, and has never been validly diagnosed. However, the palynomorphs covered by Rudolph's terminology have been formally described and diagnosed by Potonié (see Potonié 1958 p. 61) as *Abietineaepollenites microalatus* and *Pollenites labdacus* ; these specific names were subsequently assigned by Thomson & Pflug (1953) to the genus *Pityosporites*. But these form names are very rarely used in the literature ; Rudolph's terminology still persists, and without proper definition, has been frequently used incorrectly. In the Neogene however, the situation is not so bad, as there is little variation from either of Rudolph's *Pinus* types. In the Paleocene and Mesozoic, the term *Pinus haploxylon* is often used without adequate regard to these facts. Ting (1969) creates a new species of *Pinus* pollen from the North American Eocene, and gives a synonomy to " = *Pinus haploxylon* Typ. RUDOLPH. " Ting's figures seem to differ significantly from Rudolph's original material of the Bohemian Pliocene.

Two authors have recently helped to clarify the use and meaning of the two forms. Doktorowicz-Hrebnicka (1957) and Zagwijn (1960), both interpreting Pliocene material, use the term " *Pinus haploxylon*-type " for pollen with the corpus about 40 μ in greatest diameter, in which the sacci are attached to the corpus along a straight line and their height is the same as the corpus. *Pinus* sylvestris-type is of similar size, but the line of attachment of the sacci to the corpus is slightly curved, and the corpus has a greater diameter than the height of the sacci. The marginal ornamentation of the sacci is more pronounced in this form too. Results of an experiment conducted during the course of this investigation to investigate the effect of the compression on *Pinus sylvestris* pollen show no startling results. A proportional weight of 200 m. of overburden was applied for three weeks to the modern pollen, after acetolyzation and suspended on a palynologically clean clay. Although the procedure initiated several secondary folds in the pollen grains, there was no dramatic change in morphology. The morphological differences between the two forms of *Pinus* pollen seem to be due to morphological differentiation.

Re-examination of new macerations from Rudolph's original localities at Neudorf and Fonsau (now named Nová Ves and Vonsov, respectively) in the Cheb basin of northeastern Bohemia supports the interpretation mentioned above to distinguish between the two types of *Pinus* pollen. Both in the Czech material and in that from Derbyshire however, there appears to be at least two forms of *Pinus* haploxylon-type.

This confirms Potonié's (1951) division of the species into two subform-species, *major* and *minor*, which were later considered and illustrated by Thomson & Pflug (1953) as *Pityosporites microalatus* f. *major* and f. *minor*. Potonié et al. (1950) also made a distinction between small and large specimens of *Pinus* sylvestris-type. This distinction of both *Pinus* types into *major* and *minor* is solely a consequence of their size difference. It could be the result of developmental factors just as much as taxonomic ones, though the apparant absence of both *minor* types from European Miocene assemblages suggest that there is some taxonomic difference.

Previous authors of Tertiary palynology have never treated *Pinus* haploxylon-type as an important stratigraphic marker ; indeed, it is regularly distributed within the Neogene and Pleistocene (see Rankama, 1967). A review of the European literature however shows that the quantitative relationship between *P.* haploxylon-type and *P.* sylvestris-type is of significance when comparing the Upper Pliocene to the Miocene. The Upper Pliocene records which distinguish quantitatively between the two *Pinus* types all show that *P.* sylvestris-type is dominant to *P.* haploxylon-type, (Zagwijn, 1960 ; Pons, 1964 ; Leschik, 1951 ; etc.). Altehenger (1959) shows details of the proportions of the two *Pinus* forms from several German Pliocene localities. Only at localities believed to represent the lower part of the Pliocene, at Sylt, Ptolemais, Schosnitz and Wallensen, does the number of *P.* haploxylon-type pollen grains counted exceed the number of *P.* sylvestris-type. The smaller number of records from the Miocene show that although *P.* sylvestris-type can occasionally be dominant (Doktorowicz-Hrebnicka, 1957), *P.* haploxylon-type is itself most often dominant (Mazancova, 1962 ; Kremp, 1950 ; Oszast, 1960). Results from the Derbyshire assemblage pollen counts show that *P.* haploxylon-type is always dominant. As will be discussed in Section VI of this paper, this supports the Mio / Pliocene boundary age which has been attributed to the deposit.

Tsuga canadensis-type

T. diversifolia-type

(Pl. 6, Figs. 1–2)

As with the names used here to describe the two species of *Pinus* pollen, the original (and invalid) terminology of Rudolph (1935) for the two types of *Tsuga* pollen, though formally diagnosed by Thomson and Pflug (1953) as form-taxa, continues to be used in the literature. *Tsuga* canadensis-type has a narrow equatorial fringe with spinules up to 3 μ long, the whole pollen grain being up to 90 μ in diameter. It was this pollen type which Thomson and Pflug assigned to their form taxa, *Zonalapollenites viridifluminipites*, a name rarely used, perhaps for phonetic reasons. *Tsuga* diversifolia-type, described by Thomson and Pflug as *Zonalapollenites igniculus* has a more prominant equatorial fringe (up to 10 μ in width) which is deeply indented, but on average, the pollen has a smaller diameter than the other type, rarely exceeding 80 μ. Spinules are completely absent from this type.

Many attempts have been made to compare both these commonly occurring Neogene pollen forms to living species. If this were possible, then insight might be

gained on the way in which the genus has become restricted to Eastern Asia and North America. Originally, Rudolph implied that *Tsuga* canadensis-type was the same as pollen from modern *T. canadensis* which is now restricted to eastern North America, whilst the other type's affinity was to *T. diversifolia,* now occurring only in Japan. More recent palynological records (Pons, 1964) however, suggest that it is impossible to rely on these comparisons.

Szafer (1949) made a special study of this genus, instigated by the discovery of abundant macrofossil remains in the Middle Pliocene deposit at Kroscienko. He identified two species from the deposit, which are almost identical with the living *T. canadensis* and *T. caroliniana,* both modern North American species. He suggested that divergence from a primitive type occurred, perhaps during the Miocene, which gave rise to the two separate populations that are found at Kroscienko. But the two pollen types found in Derbyshire and elsewhere in the European Tertiary cannot be as closely compared to these same two living species as Szafer's macrofossils. Quite different palynological forms of the genus have been found in the North American Tertiary (Axelrod & Ting, 1960 ; Ting, 1969) suggesting that the species which have colonized Europe and the New World since the beginning of the Tertiary represent at least two distinct genetic lines.

PODOCARPACEAE ?

32. *Podocarpoidites libellus* R. Pot.

(Pl. 6, Figs. 3–4)

Although present here in small amounts, this bisaccate pollen is widely distributed in the sections studied. The corpus is thick walled with coarse wrinkles, and is less broad (30 μ) than the sacci (40 μ) which are irregularly reticulate, though this reticulum does radiate from the point of attachment with the corpus. Ting (1969) introduced the term " magnisaccate " to describe this size relation of corpus to sacci, and points out that modern magnisaccate pollen only occurs in the Podocarpaceae, never in the modern species of the genus *Pinus* that have been studied palynologically. There is some similarity however between pollen from modern *Pinus* species and that of *Podocarpus* which is of the prolate equisaccate (corpus prolate, sacci and corpus of the same height) type—a trend of parallel evolution. Such a trend might also have existed in the Tertiary with regard to the magnisaccate character, so that Ting's remark cannot be construed as demonstrating that this Derbyshire form is of the genus *Podocarpus.*

The question of the botanical affinity of this pollen type assigned to *Podocarpoidites libellus* bears on the historical distribution of the genus *Podocarpus.* Florin (1963) was of the opinion that the genus has never existed in the northern hemisphere. This view is not entirely unchallenged, especially since Dilcher's (1969) discovery of reliable *Podocarpus* leaves in the North American Eocene. But there are no other entirely irrefutable records either in North America or Europe. Mädler's material from the German Pliocene was unfortunately destroyed during the war, and his published record of *P. kinkeli* is not entirely convincing (Ferguson, 1967). The

remaining European Tertiary examples of the genus are all of the dispersed pollen, which, as explained above, might be an extant species of *Pinus*. In Europe then, no fossil material exists which can refute Florin's contention that the genus never extended north of the Tethys. There is no other gymnosperm genus represented by pollen from the European Neogene which has no reliable macrofossil record in this area to support its identification in the dispersed pollen state.

Two form species, *Podocarpoidites libellus* and *Pityosporites podocarpoides* Th. 1958 have been described from the German Miocene. The first of these has been discussed by Potonié et al. (1950). It has a length of about 55 μ and seems to differ only in size from Thiergart's species, which has its longest axis at 75 μ. The Derbyshire specimens most accurately fit Potonié's species, though the distinction between the two is very slight.

Lastly, 4-saccate pollen of the *Podocarpus* type is very common in the *Dacrycarpus* section of the modern genus. In other modern gymnosperm genera 4-saccate pollen only occurs as a rare aberrant type. Just three specimens of the 4-saccate pollen have been observed in the current investigation ; the morphology is sufficiently similar to that of modern 4-saccate *Podocarpus* pollen to compare it to this family. These specimens also give a little more strength to the argument in favour of *Podocarpus* rather than an extinct *Pinus* as the modern genus of closest pollen morphology.

PAPILIONACEAE ?

33. *Tricolpopollenites ipilensis* Paclt.
34. *T. liblarensis fallax* (R. Pot.) Th. & Pf.
35. *T. liblarensis liblarensis* (Thoms.) Th. & Pf.

(Pl. 7, Figs. 1–6)

None of these tricolpate forms have been identified *in situ*, and their tentative attribution to this family is based solely on comparison to modern members of the family by previous authors.

Tricolpopollenites ipilensis has only recently been described from the L. Miocene of Slovakia (Pacltova, 1966). This pollen type has also been identified from Miocene deposits in Germany and also from the Mio / Pliocene boundary in S.E. Bohemia (Mazancova, pers. comm.) The exoexine has a thick clavate sculpturing (at a scale making it imperceptable in the Plate), the polar axis is about 20 μ in length, the outline is prolate, and the colpi do not reach closer than 4 μ to the poles.

T. liblarensis (Thiergart 1940) Th. & Pf. is common throughout the whole Tertiary period in Europe, though the subspecies *fallax*, unlike *liblarensis*, seems to occur most abundantly in the Miocene (Zagwijn, 1960). By the Pliocene both forms occur in diminishing quantity though more often than not they are completely absent (v.d. Brelie 1961). The species has three long colpi, and a thin exine with a smooth or intrareticulate hyaline wall, with a perprolate outline. The two subspecies differ firstly in size and secondly in ornamentation ; *fallax* is less than 18 μ in length with a smooth wall, whilst *liblarensis* is larger, no more than 25 μ long, with a faintly intrarugulate ornamentation.

The natural affinity of both forms, presumably similar for the two types, has been variously suggested, or rather guessed. Thiergart (1940), profferred the Papilionaceae, an idea supported by several authors since. Potonié et al. (1950) suggest that in all probability it is a member of the Cupuliferae (i.e. Fagaceae), whilst Thomson and Pflug (1953) concede this point but alternatively suggest that it might belong to some herbaceous plant.

SYMPLOCACEAE

36. *Porocolpopollenites rotundus* (R. Pot.) Th. & Pf.
37. *P. vestibulum* (R. Pot.) Th. & Pf.

(Pl. 7, Figs. 7–9)

These two species of *Symplocos* pollen are distinguished mainly by their shape and ornamentation. *Porocolpopollenites rotundus* is more or less circular in outline with a smooth wall, whilst *P. vestibulum* has an amb with three concave sides and pronounced scabrate sculpturing. The sculpturing is often pronounced enough to give a spiny appearance comparable with some modern species of the genus, e.g. *S. setchuensis* (Erdtman, 1952, p. 424). This feature is not mentioned either in the descriptions of Potonié et al. (1950) or in the emended diagnosis of Thomson & Pflug (1953). Though some may consider it of sufficient importance to create a new species, Potonié's form species are used here with the knowledge that other investigators have adopted a broad definition to these existing taxa. Both fossil species have a vestibulum to the pores, which have very short colpi.

Although most abundant in the Miocene, pollen of the Symplocaceae has been reported from Pliocene deposits in Germany (v.d. Brelie, 1959 ; Rein, 1961), Holland (Zagwijn, 1960) and France (Pons, 1964). All three of these records show that the pollen occurs in very small quantities when present in the Pliocene, and with a morphology rather difficult to reconcile with any of the geologically older previously described species.

NYSSACEAE

38. *Nyssa* sp.

(Pl. 7, Figs. 10–11)

These prolate tricolporate pollen grains are identified by virtue of their three pores being circumscribed by caverna. The wall is smooth with no sculpturing elements and the polar axis is 20–25 μ in length. Thomson & Pflug's (1953) form species *Tricolpopollenites kruschi* is the most similar established taxa to the Derbyshire specimens, though its exine has fine intrarugulate ornamentation, a feature not observed in the Derbyshire material. Thomson & Pflug set up five subspecies of *T. kruschi* varying in the size and prominance of the intrarugulate structures, but only two of the taxa have stratigraphic importance with the Tertiary. There are very few specimens of *Nyssa* sp. pollen occurring in any of the Derbyshire deposits (only 12 such specimens have been observed), and consequently no reliable comparison to any of these subspecies can be made.

Pollen from the family occurs very commonly throughout the whole Tertiary period, but is not found in Europe after the cold period which marks the end of the Pretiglian (de Jong, 1967). The aquatic environment in which *Nyssa* now grows was not only more widespread in Europe during the Tertiary, but it is also more conducive to the production of a facies in which plant material can survive as fossil (Teichmuller & Teichmuller, 1968). These authors suggested that *Nyssa* formed a major association with *Taxodium*, to produce large areas of forest swamp, which gave rise to the autochthonous German browncoals. This situation is unlikely to have been repeated in Derbyshire, due to the absence of high pollen counts for both *Nyssa* sp. and the Taxodiaceae. As will be discussed later in Section VII, the apparent low amount of aquatic or swampy vegetation in the Derbyshire assemblage suggests that this played only a small part in the total vegetation cover of the region. Fassett (1960) points out that there are North American species of *Nyssa* which can grow on either dry or damp soils, so that there is no cause to regard the presence of that genus as indicating a swampy habitat.

ARALIACEAE

39. *Hedera* sp.
40. *Tricolporopollenites edmundi* (R. Pot.) Th. & Pf.

(Pl. 7, Figs. 12–14)

The pollen referred here to *Hedera* sp. is about 35 μ in length, elipsoid, tricolporate with caverna, and with reticulate sculpturing which is much finer at the poles than the equator. Tricolporate pollen of this reticulate type is very widely variable both as the dispersed fossil, and in material from a single modern species. It is likely that some of the forms regarded here as belonging to the genus *Hedera*, are members of quite a different group. But they are small in number in this deposit (as in all European Pliocene deposits) and are not thought to belong to important arboreal species. Thomson & Pflug (1953) described a baculate tricolporate form with affinity to *Hedera* as *Tricolporopollenites wallensenensis*. The Derbyshire specimens of *Hedera* sp. are not baculate ; indeed, Altehenger (1959) reports a conversation with Thomson in which the latter concedes that *T. wallensenensis* might belong to some other genus within the Araliaceae. Certainly all species of *Hedera* pollen examined by the author are reticulate rather than baculate.

The genus has only once been recorded in Europe from strata older than Pliocene (Pacltova, 1966). In the Pliocene itself, Altehenger (1959) records at least four localities in the Upper Pliocene of Germany with reticulate pollen of *Hedera*, whilst Pacltova (1963) has found similar types at Ledenice, Southern Bohemia. The genus is well represented in the Pleistocene from several interglacials. Godwin (1956) has discussed the implications of the delicate climatic requirements of *Hedera helix* : that it cannot withstand exceptionally hard present-day British winters, when the temperature falls below $-1{\cdot}5$°C as average for the coldest month (Iversen, 1944). This living species is consequently associated with oceanic climates in the temperate latitudes.

Tricolporopollenites edmundi can be easily identified : its most characteristic feature being the large baculae up to 3 μ in length, the entire wall being up to 8 μ in thickness. Zagwijn (1960) regards the sculpturing as clavate, occasionally merging to give an apparent negative reticulum. The species is very rare in the Derbyshire assemblage but it is nevertheless of considerable stratigraphic significance. The form is typical of European Miocene deposits (Potonié, 1967), though it occurs also in the Oligocene and the Lower Pliocene. Zagwijn (1960) has found regular though very small quantities in the Susterian and Branssumian of Holland, and Mazancova (pers. comm.) has similar quantities in her Mio / Pliocene assemblage from Jihlava, S.E. Bohemia. Pons (1964) records the species from the most recent Pliocene deposits (Middle / Upper Pliocene) of La Bégude and Mollon-Ravin in southern France, though this of course is more than 1,000 Kms. south of these other records in Holland and Derbyshire, which may be correlated with its higher stratigraphic position. The absence of this pollen type from Upper Pliocene deposits of Central and Western Europe provides further support for a Lower Pliocene age to the Derbyshire Flora. In an extensive comparison of this fossil pollen with that from modern material, Mamczar (1962) has concluded that *T. edmundi* shows greatest resemblance to pollen from the genus *Aralia*.

HAMAMELIDACEAE

41. *Liquidambar* sp.

(Pl. 8, Fig. 1)

This pollen, similar to that described by some authors as *Periporopollenites stigmosus* (R. Pot.) Th. & Pf., is about 40 μ in diameter, and the exine is intrarugulate with distinct though very small columellae. More recently, Krutzsch (1966) has submitted a revised diagnosis of this form species based on the structure of the pores, and corresponding well to the Derbyshire material. Pollen, described as either *P. stigmosus* or *Liquidambar* sp., has been commonly identified from the whole Tertiary of Europe, and has been well reviewed by Potonié (1967). The genus did not return to northern and central Europe after the first cold period of the Pretiglian following in this respect the behaviour of the taxodiaceous genera and *Nyssa*, with which *Liquidambar* is regularly associated in modern environments.

Kouprianova (1960) has traced the palynological history of the modern genus right back to the Cretaceous. She has identified four of the modern species from Miocene or Oligocene desposits and has suggested that recognizable fossil species have linked these four to an original subtropical member of the genus from which all these other species evolved. However, there is no reference in her scheme to the pollen type present here. Thomson & Pflug's form species is not so narrowly defined as are Kouprianova's species ; indeed, *P. stigmosus* could well be synonymous with all the species that Kouprianova mentions. But implications do arise from the ecological associations of both the modern species of *Liquidambar* and of Kouprianova's species. *L. formosana* and *L. macrophylla* both grow in the far east with genera such as *Pinus*, *Cryptomeria*, *Tsuga* and *Quercus* ; plants which are present in the Derbyshire fossil

assemblage. *Liquidambar angaridae* Kouprianova from the Lower Oligocene of Western Siberia is also a member of a similar group of plants to those represented in the Derbyshire assemblage.

SALICACEAE

42. *Salix* sp.
43. *Tricolpopollenites retiformis* Th. & Pf.

(Pl. 8, Figs. 2–3)

The " salicoid " pollen of the European Tertiary is so diverse, especially in the nature of the exine ornamentation, that there are likely to be numerous genera and species represented, not necessarily of this family. The pollen referred here to *Salix* sp. is finely reticulate, each lumen being about 1 μ in length. This form is comparable to the " *Salicoid* " form mentioned by Zagwijn (1960) from the Dutch Pliocene (verbal commn.). Apart from his record, the type is difficult to trace in accounts from other Neogene deposits, due to the close similarity of so many tricolpate forms of this size (about 25 μ long, prolate). For instance, it is often difficult, especially when preservation is bad, to distinguish between this form with very fine reticulation and other intrabaculate forms assigned to *T. microhenrici*. Certainly it is difficult to point to any differences between the Derbyshire *Salix* sp. type and certain of Thomson and Pflug's (1953) illustrations of *T. microhenrici*.

The other pollen type assigned to the Salicaceae corresponds to the form species *Tricolpopollenites retiformis*. Thomson & Pflug (1953) suggested that its botanical affinity was to either the Salicaceae or the Platanaceae, though subsequent assignations have been made solely to the former family. This tricolpate pollen is up to 35 μ in length and has a baculate surface with an extremely thin nexine. Widespread variation in the size of the baculae is common not only in the English material but also in that from Germany and elsewhere. Though distinct from the form referred here to *Salix* sp., other authors have used this modern generic name to describe pollen indistinguishable from that of *T. retiformis* (Pons, 1964 ; Leschik 1954 ; Neuy-Stolz, 1958 ; Pacltova, 1963). At least the baculate form seems to have been more widely distributed than the form referred here simply to *Salix* sp.

MYRICACEAE

44. *Myrica* sp.

(Pl. 8, Fig. 4)

This triporate pollen is best distinguished from other pollen with this basic morphological feature by the presence of the atrium at each pore ; that is, the area in which the endexine is absent from the pore region. This point of distinction can only rarely be used in conducting pollen counts however, as bad preservation and oblique orientation often hide the feature. Other distinguishing characters such as

size, shape and sculpturing, mentioned by Zagwijn (1960), are also regularly obscured and cannot be relied upon to make quantitative determinations in Tertiary material. But Romanowicz (1962) has produced evidence which suggests that *Myrica* pollen is more abundant in the European Neogene than any other triporate pollen. She differentiated ten forms of the genus, and compared some of these to pollen from such modern species as *M. javanica*, *M. carolinensis*, and *M. gale*.

Pollen from the genus has been regularly identified from both Neogene and Pleistocene deposits throughout Europe. The extant European species of the genus, *M. gale* (the bog myrtle), is characteristic of fens and bogs, often succeeding *Sphagnum* and *Calluna* associations. The chief genera which ecologists associate with *M. gale* in the modern environment were seemingly present in Derbyshire during the Lower Pliocene.

BETULACEAE

45. *Alnus* sp.
46. *Trivestibulopollenites betuloides* Th. & Pf.

(Pl. 8, Figs. 6–7, 9–10)

The *Alnus* pollen present in the assemblage has four or five pores with the characteristic arci connecting adjoining pores. Observations on modern species show that the number of pores varies within a single species, so that the fossil material could represent just one species. Other features vary within single species of this genus, for instance the wall thickness—a character used by Doktorowitz-Hrebnicka (1964) to separate fossil remains of *Alnus* pollen into twelve " forms ". The single form species *Polyvestibulopollenites versus* (R. Pot.) Th. & Pf. has been applied to numerous specimens of the *Alnus* type pollen in the European Tertiary ; pollen which seems to be identical with that from the Derbyshire deposits. Both Thomson & Pflug (1953) and Krutzsch (1957) point out that the genus was rare in Europe during the Paleogene, but increased during the Neogene to reach a maximum during the Pleistocene.

Examination of acetolysed pollen of some of the modern species of *Betula* shows little variation within the genus. The pollen is distinctive enough to assure accurate identification of the genus ; triporate, with each pore protruding and distinctly vestibulate. The fossil material from Derbyshire that can be assigned in this way to *Betula* spp. has great variation in both size and shape. If the species uniformity seen in the modern pollen prevails in the Neogene material, then there are several species of the genus represented here. But there is substantial difficulty encountered even by Quaternary botanists in distinguishing between pollen of the modern British species (Birks, 1968). In the light of this possibility, the betuloid forms are here referred to by the form name *Trivestibulopollenites betuloides*. Thomson & Pflug's diagnosis allows quite a wide variation in both size and shape (" 18–35 μ. Contour roundish . . . ") so as to accommodate all the forms found here. The problem has been dealt with in other ways by Tertiary workers : Doktorowitz-Hrebnicka (1964) described 14 " forms " of *Betula* species, Macko (1957) compared to modern species, whilst the majority of authors have assigned the pollen to either *Betula* sp. or else to the form taxon used here.

FAGACEAE

47. *Tricolpopollenites microhenrici* (R. Pot.) Th. & Pf.

(Pl. 8, Figs. 11–13)

This important Neogene taxon was introduced by Potonié (1931) (as *Pollenites microhenrici*) who regarded the pollen as tricolporate. In their revised diagnosis, Thomson & Pflug reinterpreted the pore structures as geniculi, which they explained are often absent altogether. Indeed, geniculi are often difficult to discern even in modern pollen grains which are reputed to possess them. The significance of the geniculus (*sensu* Thomson & Pflug) in the evolution of pollen morphology has been briefly mentioned by Doyle (1969) who suggests that the presence of a geniculus represents a primitive colporate condition. *T. microhenrici* could well represent an even more primitive state in that the geniculi are not always present. Perhaps the scanning electron microscope can help to solve this problem. Before 1953, several authors used the generic name *Quercoidites* for this pollen, based on the species *henrici* which shows a geniculus (Potonié et al. 1950). In their diagnosis of the form species, *Tricolpopollenites microhenrici*, Thomson & Pflug also describe the exine ornamentation as intragranulate or intrabaculate, a character which is evident in the Derbyshire specimens.

Small tricolpate and tricolporate pollen grains are traditionally extremely difficult to identify and describe accurately, mainly because there are so few variable characters. Size, shape, exine ornamentation and length of colpi are so often the only criteria available. Consequently, many important arboreal and herbaceous genera are most difficult to identify by current palynological techniques, and most of these are represented in the extant flora by numerous species. So not only is there inevitable variation in the form of *T. microhenrici* as diagnosed by Thomson & Pflug and shown in their photographs, but also, any attempt to seek a modern botanical affinity is likely to be extremely unreliable . The Derbyshire material presents no exception to this, and it is often difficult to distinguish between the various tricolpate forms occurring in the assemblage. Although the diagnosis of *T. microhenrici* adequately describes many of the specimens from this assemblage, there is some variation especially in the shape and nature of the colpi. Indeed, some authors of Tertiary palynology would use this variation as a basis for several new species. It is also occasionally difficult to observe the nature of the exine ornamentation, so as to distinguish between this type and *T. liblarensis*.

Most authors are in agreement however, that *T. microhenrici* is most likely to have affinity with pollen of the modern genus *Quercus*. The pollen has a similar morphology to that from some modern tropical and subtropical species of the genus, and Pons (1964) has stressed similarity to the southern European species *Q. mediterranea*.

In view of the variation in the form of this tricolpate pollen type, any comparison between different authors' records, even within a limited area such as Europe, must inevitably have limitations. Pliocene records of *T. microhenrici* in Europe are very rare. Zagwijn (1960) found a very small number of this type in the Lower Pliocene deposits of Holland, whilst further south in the Rhodanienne, Pons (1964) identified

a significant percentage of pollen from four species of *Quercus*, including that which he referred to *Q. mediterranea*. Reviewing the German records of *T. microhenrici* however, von der Brelie (1967) showed that the species has never been recorded there from the Pliocene, so that it may accordingly be regarded as a consistent member of the component typical of Miocene assemblages. Other German authors too (Potonié, 1931 ; Thomson & Pflug, 1953) restrict the species range to Oligocene and Miocene deposits, whilst Zagwijn (1960) has found it as an abundant member of Miocene floras in Holland.

The occurrence of *T. microhenrici* in this Derbyshire assemblage of presumed Mio / Pliocene boundary age can be reconciled with the European data, especially in the light of Zagwijn's record from an approximately equivalent horizon. What is not so easy to explain in terms of this age determination however, is the large percentage occurrence of the form in the samples from the Bee's Nest pit (Fig. 5). If the Derbyshire form is identical with that from the Continent (an assumption by no means certain, as implied above when discussing the variation within the form species) then the more oceanic climate of Derbyshire during Neogene times might account for the more abundant occurrence of the type here.

CORYLACEAE

48. *Corylus* sp.
49. *Carpinus* sp.

(Pl. 8, Figs. 5 & 14)

The pollen from both these genera is very common throughout the whole Tertiary period ; in Britain both have been identified palynologically from the Lower Tertiaries of southern England (Chandler, 1964) and from just a small number of Quaternary sites. *Corylus* is most easily identified by its simple germinal aperture, having no separation of the ectexine from the endexine. *Carpinus* has 3–5 pores, most commonly four, with a thin chagrinate exine. In this investigation, no attempt has been made to separate either genera into consistent species, whilst in quantitative analysis, it has often proved to be impossible to separate *Corylus* from *Myrica* due either to poor preservation at the pore region, or else to an oblique orientation of the grain in the glycerine jelly.

JUGLANDACEAE

50. *Juglans* sp.
51. *Carya* sp.

(Pl. 8, Figs. 15–16)

Juglans pollen has been recorded both from British Interglacials (Godwin, 1956) and from the Oligocene beds of S.E. England (Chandler, 1964), so its occurrence here is not surprising. Krutzsch (1957) shows that this type of pollen is most abundant in Germany in deposits of Miocene age, whilst further west in Holland, Zagwijn (1960) has recorded the genus only from Pliocene and Pleistocene strata.

The Derbyshire material is extremely rare and has up to eight sub-epuatorial pores, and a diameter of about 30 μ.

Carya on the other hand, has been found in Europe no higher than the Tiglian (Zagwijn, 1963) and though it occurs in the Paleogene (in small quantities) it is regarded as an important component of the European Neogene. It is rarely absent from Pliocene and Miocene pollen assemblages throughout Europe though it attains a slightly higher quantitative occurrence in the Pliocene (Altehenger, 1959 ; von der Brelie, 1959 and 1967) and for this reason is included by both these authors in the Pliocene element (see Section VI).

Thomson and Pflug (1953) compared five of their form taxa to the genus, but each type has a similar stratigraphic range, so that the subdivisions have little value at the present. Zagwijn has mentioned a form with a relatively thin exine and with more or less equatorial pores, which he says is generally restricted to the Tiglian : this form is not met with in the Derbyshire material.

The ecological implications of the occurrence of *Carya* have been mentioned by Chaloner (1968) when discussing the presence of the genus in the Paleogene of S.E. England, suggesting that it occupied the wooded hinterland rather than the *Nipa* swamps which are generally associated with the deposition of the London Clay. The genus's common occurrence in Europe during the Tertiary makes an interesting comparison to the present distribution pattern, some species being restricted to North America whilst the others are limited to S.E. Asia. It is unlikely that palynology will ever be able to provide accurate specific identifications of the fossil material in terms of the extant species, with the object of relating the European occurrence with those of either the Old or New Worlds.

ULMACEAE

52. *Ulmus* sp.

(Pl. 8, Fig. 8)

The genus is commonly recorded throughout the European Tertiary and Pleistocene. In most Neogene records, including this one, the pollen is present very infrequently. The pollen grains are about 25 μ in diameter, coarsely rugulate, with up to ten irregularly spaced pores.

AQUIFOLIACEAE

53. *Tricolporopollenites iliacus* (R. Pot.) Th. & Pf.
54. *T. margaritatus* (R. Pot.) Th. & Pf.

(Pl. 9, Figs. 1–2)

Both these types have been regularly determined from the European Tertiary and though they have no particular significance to the stratigrapher, their botanical affinity to the modern genus *Ilex* is certainly enough to enable climatic conclusions to be made. Fossil leaf material of the modern genus has been determined from the German Pliocene by Mädler (1939).

Tricolporopollenites iliacus has very prominant clavate sculpturing which tends to conceal the pores and colpi. Thomson & Pflug (1953) separated the form species into two form subspecies on the basis of their size, f. *major* having a longitudinal dimension greater than 45 μ whilst f. *minor* is from 25–45 μ. Both forms have been identified from the Derbyshire assemblage. Pons (1964) suggests affinity of this form species to *Ilex aquifolium*, pollen of which has been commonly described from Pleistocene deposits ; the same modern species was determined by Mädler for his macrofossil material. Three fossil species of the genus are mentioned by Gothan and Weyland (1964) in reviewing the macrofossil record, though only one of these is from the Neogene.

Tricolporopollenites margaritatus has much smaller clavate structures than the previously mentioned type, and is about 30 μ in length. Pons (1964) compares this form taxon with the Recent *Ilex canariensis*. But this and other attempts to relate either the fossil pollen or leaves of this plant to modern species is tentative, despite the unusually distinctive characters of the material. Both *Ilex* and another genus represented in the Derbyshire assemblage, namely *Hedera*, are useful climatic indicators. Experiments on both these genera (Iversen, 1944) show that the modern European species are intolerant of a mean monthly temperature which falls below −0·5°C. The implications of this are reflected in the distribution map of the species (Godwin, 1956), where the plants are shown to be absent from northern and continental Europe—regions of low oceanicity. In the fossil record however, there are Tertiary records of the genus from parts of Europe that are continental in climate (Pacltova, 1966 ; Mazancova, 1962—both in Slovakia ; Doktorowitz-Hrebnicka, 1964—Poland). A similar state of affairs has been explained for *Tsuga*, though in that case, the possibility that the European occurrences are of an extinct species favouring more diverse climates is another possible explanation. Alternatively, Central Europe may have had less severely cold winters than now, or else the fossil species of these genera were able to withstand lower temperatures than the extant ones.

SAPOTACEAE

55. *Tetracolporopollenites sapotoides* Th. & Pf.

(Pl. 9, Fig. 3)

Thomson & Pflug (1953) made tentative comparison of seventeen taxa to this family ; this diversity, together with the form's similarity to the tricolporate *Nyssa*-type (Doktorowitz-Hrebnicka, 1964 identified very similar tetracolporate pollen as *Nyssa*) make any comparison to modern genera rather dubious.

The occurrence of pollen from this family is mainly restricted to the European Miocene (v.d. Brelie, 1967 ; Potonié, 1967) though Pons (1964) has made one of the few determinations from Pliocene strata. This Derbyshire record represents the youngest record of the family in the more northerly latitudes of Europe.

ERICACEAE

56. *Empetrum* sp.
57. *Calluna* sp.
58. *Erica* sp. ?
59. *Rhododendron* sp. ?

(Pl. 9, Figs. 7–11)

Although the recognition of pollen from this family is a simple matter—in most of the genera the pollen grains are united as tetrads—distinction at the generic level has never been fully investigated. One of the fullest accounts of the pollen morphology of extant members of the family has been given by Oldfield (1959), whilst for Tertiary material, most authors do not even attempt to refer specimens to living genera. In these cases, use is most often made of the form taxa *Tetradopollenites callidus* (R. Pot.) Th. & Pf. and *T. ericius* (R. Pot.) Th. & Pf., which have been described throughout the European Tertiary.

In the Derbyshire assemblage, pollen of the Ericaceae forms a very high percentage of the total pollen count (Fig. 6) and examination of the material reveals at least four morphological types. Comparison of these forms to modern reference material was found to be of little value due to the great variation in pollen morphology within each very large genus. The identifications that have been made here are based on the conclusions of Oldfield's work.

Pollen tetrads assigned to *Empetrum* sp. are of compacted shape, often rounded or sub-triangular, with thick inner walls. The exine has a finely verrucate ornamentation, whilst in most specimens in the Derbyshire material both the pore and furrow were indistinct.

Calluna sp. tetrads have been identified by their loose and irregular shape. The exine, which is thinner than in the other tetrad genera of this family mentioned here, has an irregular verrucate ornamentation.

Both *Erica* and *Rhododendron* have a very large number of modern species and distinction of their pollen tetrads is difficult even at the generic level. The recognition of the two separate genera in this assemblage must be regarded as tentative. Chief among the apparent differences in pollen morphology of the two genera is the nature of the exine. In *Erica*, ornamentation is very faint, whilst the walls of *Rhododendron* tetrads are prominently reticulate.

ONAGRACEAE

60. *Corsinipollenites maii* Kr.

(Pl. 9, Fig. 5)

The easily recognized triporate pollen from plants of this family usually occur in Tertiary deposits in very small quantities. Though present throughout the whole Tertiary in Europe, most form taxa have been described from the Pliocene (Krutzsch, 1968).

Although some modern species in the family are trees and shrubs, the great majority, including those living in and around Europe, are of herbaceous habit. If,

as seems likely in this case that the pollen is from a herbaceous plant, then it represents one of the few instances of plants of this habit (among the dicotyledons) that have been identified from the Derbyshire assemblage. There are without doubt pollen grains from many other herbaceous genera that have been examined and passed unidentified in the Derbyshire material ; but they are of very rare occurrence, and are dissimilar from any previously described material. Rather than formally describe and illustrate these forms, to no currently useful geological or botanical purpose, the forms are not mentioned qualitatively in this work.

COMPOSITAE

61. *Compositoipollenites rizophorus* R. Pot.

(Pl. 9, Fig. 4)

Another rarely occurring herbaceous plant record is of pollen from the Compositae. The pollen is about 20 μ in length, covered with spinules up to 3 μ in length with a swollen base. Enough is known of the detailed palynology of this family (Wodehouse, 1935) to justify no generic assignation being made. Few modern species of the family are trees or shrubs however, suggesting, along with the infrequent occurrence of the pollen in this Derbyshire material (and in other Tertiary assemblages) that the parent plant was of herbaceous habit.

A number of Tertiary pollen assemblages refer to this type as Compositae-type, though Potonié (1960) based the name used here, *Compositoipollenites rizophorus*, on type material from the Eocene of the Geiseltal. This is similar enough to the Derbyshire specimens to allow the use of this name here. *Pollenites echinatus* Pot. & Ven. (1934), similarly assigned to this family by some authors (Potonié et al., 1950) is larger than the Derbyshire specimens, with longer and broader spines.

LILIACEAE

62. *Periporopollenites echinatus* (Wodeh.) Th. & Pf.

(Pl. 9, Fig. 6)

Wodehouse's (1933) original description of *Smilacipites echinatus* suggests a likely similarity of these pollen grains to those from the genus *Smilax* ; an assignation endorsed by Thomson & Pflug (1953). The rare Derbyshire specimens have the same type of spines ; and since leaf material of the genus *Smilax* has been identified from cuticle remains in the same deposits, the assignation is further supported by this study. The Derbyshire material of *P. echinatus* is distinguished from composite pollen by its precisely spherical shape, fewer spines per unit area, the absence of 3 colpi, and the lack of a basal thickening to the spine structures. The only other fossil pollen of possible relation to the genus *Smilax* which has been previously recorded from the European Neogene is that referred to *P. echinatus* by Neuy-Stolz (1958). Macro-fossil material however has been described as *Majanthemophyllum petiolatum* (Web.) Wey., from the German browncoal (Weyland, 1957), whilst leaves

of the modern mediterranean species *Smilax aspera* have been found in the Italian Pleistocene.

GRAMINAE

63. *Graminidites media* Cookson 1947.

(Pl. 9, Figs. 12–13)

These pollen grains are up to 35 μ in diameter, have a single protruding pore, with a minutely tegillate exine. The earliest reliable palynological record of pollen from this family is from the Lower Oligocene of New Zealand (Couper, 1960) though Chandler (1964) has reported possible leaf remains from the Palaeocene of southern England. Throughout the Neogene of Europe, this pollen, as in Derbyshire, occurs in very small numbers, though it is of very wide geographical distribution.

V. QUANTITATIVE ANALYSIS

The Derbyshire Localities

A brief description of the deposits which bear the palynological assemblage has been given in an earlier publication (Boulter & Chaloner, 1970). Plant bearing grey clays, overlying variously coloured clays and sands have been found at Bee's Nest pit Brassington, and again some 7 Kms. to the north west at Kenslow Top pit, Friden. The fossil remains are found only at these two of the sixty or so of the sink-hole deposits ; these are all thought to have formed by collapse of the sands and clays into sink holes in the Carboniferous limestone which outcrops in this part of north Derbyshire and east Staffordshire. Ford & King (1968, 1969) have documented geological evidence to explain the mechanism of the deposits' origin. During the Tertiary, the limestone, with well developed solution cavities, was covered with sands and clays. Plant fossil remains survive in the uppermost clay, which is thought to have been deposited towards the end of this period. Intermittent collapse of the cavities is thought to have let down the Tertiary cover to produce the infilled sink hole structures, which are currently being worked for the silica sands. Comparable catastrophic events have been observed recently (Foose, 1967) in South Africa, producing a similarly disorganized infill of sediment in limestone sink holes.

The form of the plant bed at Kenslow Top pit is different in several respects to that at Bee's Nest pit, though the relation of each bed to the underlying clays seems to be comparable. At both localities, the plant bearing clay lies above a paler grey clay, and is situated in the estimated centre of each sink hole. The Bee's Nest deposit is much smaller than that at Friden ; on the surface at the present time, about 9 square metres is all that is exposed. Throughout the whole deposit, dark grey pollen bearing clay is mixed with the same kind of pale grey unfossiliferous clay which underlies the plant bed. In no part of this plant bed at Bee's Nest pit has an uncontaminated block of fossiliferous clay larger than about 10 cu. mls. been found ; throughout the whole deposit both horizontally and vertically, pieces of plant bearing clay are graded within the pale grey clay matrix, as shown in Figure 2. Consequently it has not been possible to obtain a series of samples which are consistent with conventional

deposition of a continuous nature. Quantitative comparisons have been made of samples from different positions in the deposit, but they show little variation from the single set of results given below in Figure 5. Towards the edge of the Bee's Nest plant bed, the number of fossiliferous pieces of clay suddenly diminishes without apparent bedding changes, to be completely replaced by the pale grey clay matrix (Fig. 2).

The plant bed at Kenslow Top pit is exposed for some 25 metres at the working

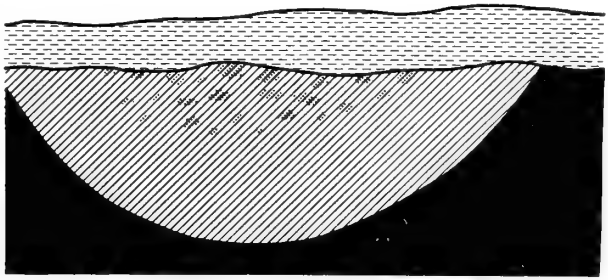

FIG. 2. Postulated section across the plant bed at Bee's Nest pit, Brassington. The plant bearing clay (stippled) is in the form of small blocks up to 100 mms. across, mixed into pale grey unfossiliferous clay (diagonal lines). The bedding of the underlying sands and clays (solid black) is folded to form a geosynclinorium. Before excavations began, the bed was covered with 2–3 metres of glacial till (dotted lines). The figure is not drawn to scale ; at present, about 9 sq. m. of plant bed is exposed.

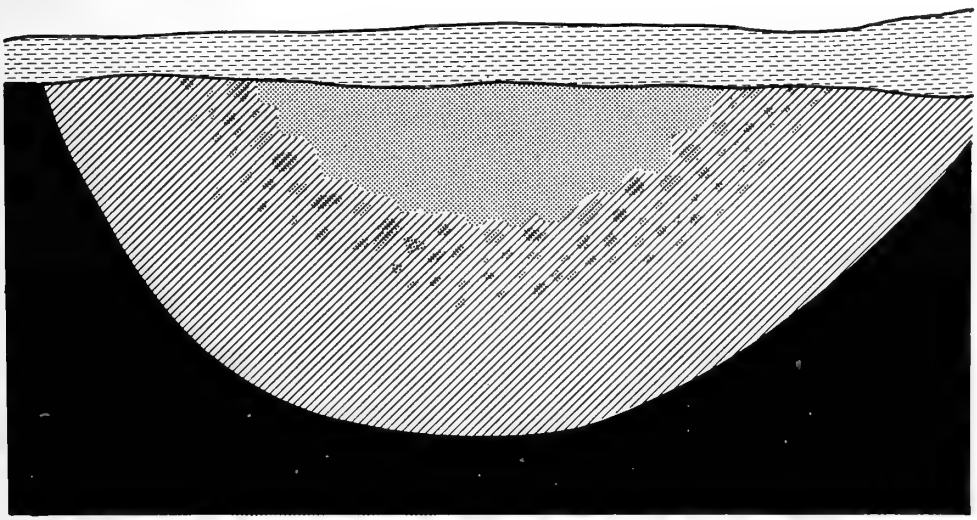

FIG. 3. Postulated section across the plant bed at Kenslow Top pit, Friden. The plant bearing clay (stippled) is in the form of a plano-convex lens, about 6 m. wide and 3 m. thick at the centre. At the lower edge of this block small pieces of plant bearing clay are mixed in with pale grey unfossiliferous clay (diagonal lines). The bed is covered with 2–3 metres of glacial till (dotted lines).

face of the pit, though debris and overwash cover the exposure at one end so concealing the true horizontal extent of the once exposed face. Information that has been obtained from quantitative palynological analysis of samples from both the horizontal extent of the exposed face and from a vertical section of the deposit make

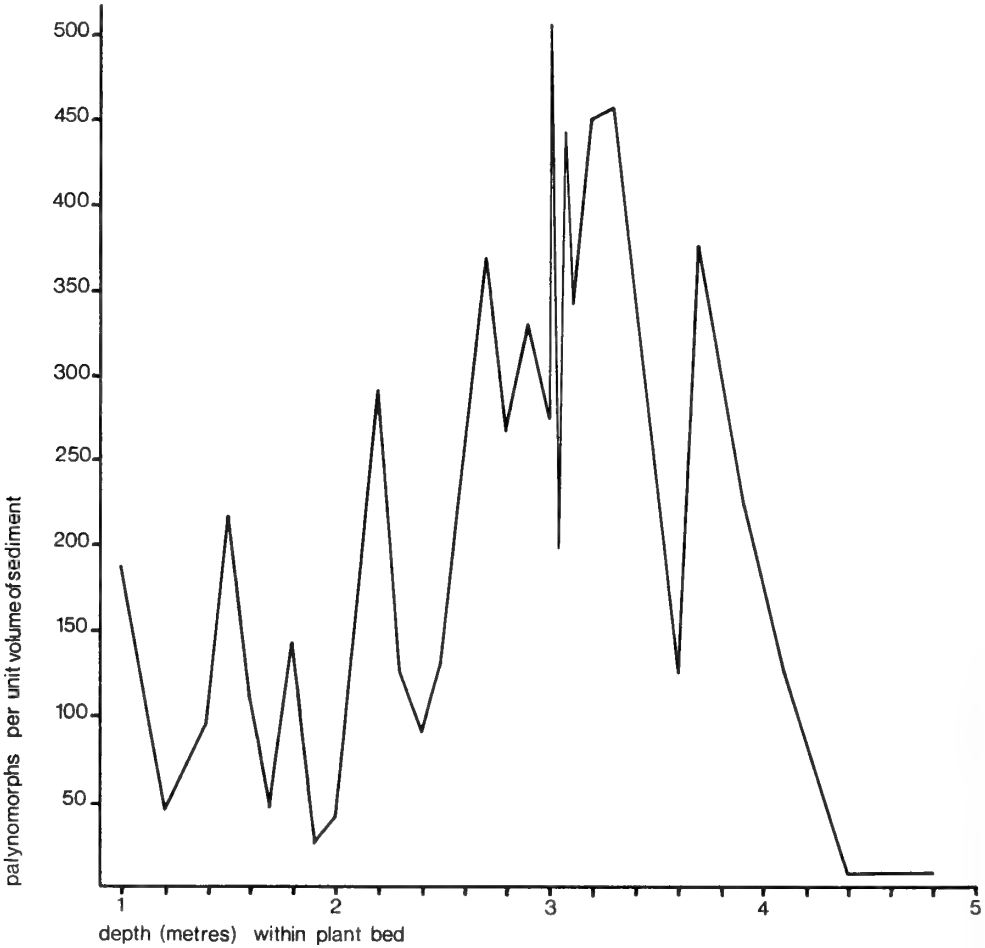

FIG. 4. The change in Absolute Pollen Frequency with depth at Kenslow Top pit. Count of the total number of pollen and spores were obtained from macerations of samples taken every 80 mm. through most of the section, though at the 3 metre depth, samples from every 10 mm. were used. Details are given in Section III of the way in which a standard volume of clay was macerated to produce preparations of comparable pollen and spore concentration.

this site more informative than that at Bee's Nest pit. The larger plant bed at Kenslow Top pit suggests that more of the plant bearing clay was let down into this sink hole during the process of collapse. The plant bearing bed here is not only thicker but the upper part has a smaller proportion of pale grey clay, whilst the lower

part is made up of irregular patches of pale and dark grey clay. The apparently plano-convex lens-shaped block has a much higher concentration of palynomorphs than that of the surrounding mixed material (Fig. 3). It is about 6 metres in horizontal extent (along the exposed face) and a borehole which has been sunk in the central part shows its thickness to be about 4 metres. Analysis of the pollen and spores from this borehole shows sudden changes in their concentration within the sediment (Fig. 4), whilst the relative proportion of different species remains remarkably constant. Examination of the deposit itself reveals no regular bedding planes *in situ*. The plant bearing clay which surrounds this lens shaped portion both laterally and below is itself mixed with the paler unfossiliferous clay in much the same way as that at the Bee's Nest locality. This mixed material is up to 4 metres in thickness, and maintains a much reduced concentration of palynomorphs (Fig. 4, $4\frac{1}{2}$ m. depth). The concentration is low even in the small patches of purely plant bearing clay, whilst the pale grey clay mixed with it is completely unfossiliferous. The low concentration then is not necessarily due only to the effect of mixing, but also to a slight facies change which itself caused a change in clay colour from pale grey to the darker browner grey colour of the plant bearing material.

Kenslow Top pit, Friden.

Macerations have been made by the methods described in Section III from samples collected from the surface of the exposure, and from the borehole mentioned above. This has lead not only to a quantitative analysis of the assemblage both horizontally and through the section itself, but also to a comparison of the concentration of the palynomorphs in each clay sample. The graph (Fig. 4) plotting the number of pollen grains per unit area against depth shows seven peaks when samples are macerated from every 80 mms. To check the consistency of this variation, samples from each 10 mms. along a small part of the borehole section were macerated (Fig. 4, 3 m. depth). The results show that there are many more peaks than are shown from the more widely separated samples. Nevertheless, it is thought that sufficient results have been obtained to show that the palynomorph concentration is very variable in vertical section.

Bee's Nest pit, Brassington.

Since the plant bearing clay at this deposit is of smaller proportions and more completely mixed with unfossiliferous clay, no samples have been obtained from a productive sequence. Those that have been examined come from parts of the flat exposed surface of the deposit and also up to 1 metre below the surface, and are, in each case, mixed with the unfossiliferous pale grey clay. The concentration of palynomorphs in these samples is variable but in no apparently meaningful way, due to the complex mixing that has occurred. Quantitative analysis of the major taxa from the samples examined produces results similar to those shown in the histogram for sample V.55635 (B.M. number) (Fig. 5).

Interpretation of the absolute pollen frequency (A.P.F.)

The results of A.P.F. counts from samples in the vertical section at Kenslow Top

pit have been mentioned above, and are recorded in Figure 4. There is insufficient evidence available to make any indubitable interpretation of the variation in the palynomorph concentration, though several suggestions can be briefly mentioned.

The method of origin of the sink hole deposits may have been responsible for the variation, in which case the geomorphological events that led to the formation of the sink hole deposits would be of significance in any interpretation. These events themselves however, are controversial (Boulter & Chaloner, 1970) though it seems most likely that collapse occurred during the Tertiary (Ford & King, 1969) rather

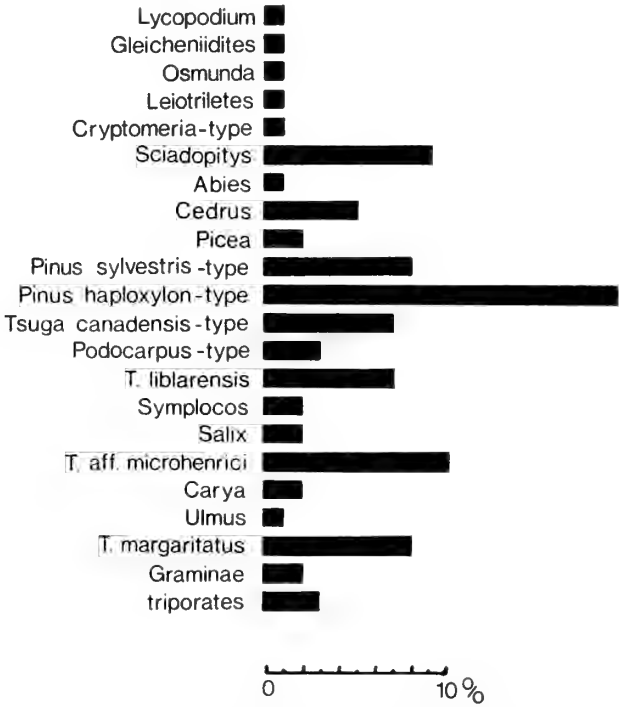

FIG. 5. Histogram showing the percentage occurrence of pollen and spores in clay sample V 55635 from Bee's Nest pit, Brassington. There was no significant variation from these results in other samples from that deposit that have been analysed.

than earlier (Kent, 1957). There is no firm evidence to confirm that the plant bearing clay either slumped into the sink holes together with the other unfossiliferous sands and clays, or whether the plant bed was deposited above the pale grey unfossiliferous clay soon after collapse had occurred. Quantitative results show that despite the change in Absolute Pollen Frequency, the concurrent composition of the assemblage is constant. In view of this constancy, had the plant bed collapsed into the sink hole at the same time as the underlying clays and sands, the sediment may have become distorted by mixing and cracking, with subsequent weathering producing the present fluctuating concentration of palynomorphs. On the other hand,

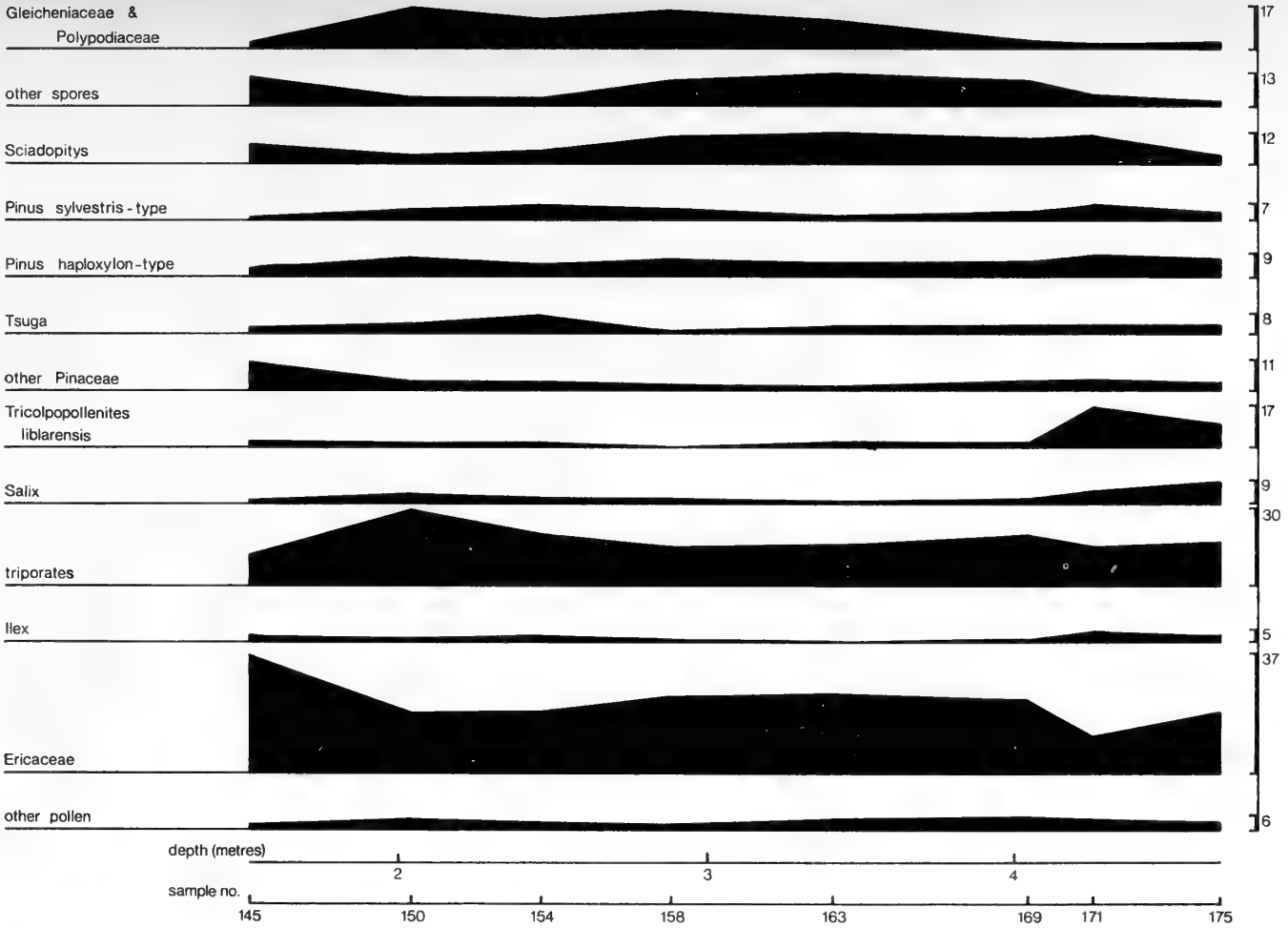

FIG. 6. Pollen diagram through the section at Kenslow Top pit, Friden. Values showing the depth within the section were measured from the base of the glacial till, and the column to the right of the diagram shows the maximum percentage occurrence of each type.

had the plant bed been deposited after collapse, reworking from the immediate vicinity of the infilled sink hole, with (seasonal ?) variations in the rate of deposition, could have produced the changes in the A.P.F. that have been recorded.

Other interpretations of the change in A.P.F. can be made on the assumption that the geomorphological events that may have occurred did not have a direct influence on the distribution of the plants in the deposit. Climatic variation and forest fire are thought to have been common events in Europe during the Neogene (Ahrens & Lotsch, 1967 ; Teichmuller & Teichmuller, 1968) and are characterized by changes in both the rate of pollen production and the type of vegetation cover. However, results from quantitative analysis of individual members of the assemblage show little change throughout the section (Fig. 6), so that such explanations are most unlikely. Details of the changes in A.P.F. show that at the 3 metre part of the section, the palynomorph concentration was at a maximum. The proportion of the warmth-loving Tertiary Component (see Section VI) increases here too, suggesting that there may have been a climatic fluctuation at the time represented by this part of the section, even if the absolute change were explained by a decrease in the rate of deposition with a consequent increase in the A.P.F.

Comparative interpretation of the quantitative analysis

For purposes of this analysis, it has been necessary to compromise on the recognition of many of the pollen and spore types. At many horizons it is not always possible to assign all specimens to one of the taxa reported above. This is due to the frequently obscure specimens in the maceration samples, which are often badly preserved, broken, or hidden by detritus. For example, distinction between *Myrica*, *Corylus* and some specimens of *Betula* necessitates perfect preservation of the exine at the pore regions ; the pores must not be obscured in any way. This ideal situation is rare in practice, so that although the distinctive features of each type are occasionally available (from which specimens the qualitative descriptions in Section IV have been made), all three types are grouped together for quantitative purposes. It has been possible to designate these groups so as to keep separate not only the members of the Tertiary Component, but also what can be regarded as the most plausible major ecological associations. So it is hoped that despite the hazards of grouping different taxa together, significant conclusions can still be made from the quantitative results.

Although the two Derbyshire deposits are separated from one another by only 7 Kms., a comparison of the quantitative results shows important differences in their floristic character. The Kenslow Top assemblage represents two distinct associations : heath and woodland. The heathland element contains plants from the Ericaceae, *Myrica, Salix, Sphagnum, Lycopodium* and some conifers, whilst the woodland is made up of the conifers, deciduous trees and ferns, such as *Lygodium, Polypodium, Gleichenia* and *Pteridium*. The ecological implications of these associations will be discussed in Section VII. Pollen analysis from the Bee's Nest pit however, shows an absence of pollen from the Ericaceae, and lower values of both spores and triporate pollen. The increased values for pollen from the woodland association suggest that this is the only environment which became preserved here.

During the time represented by the 3 m. maximum A.P.F. in the Kenslow Top section, the woodland association forms a larger part of the total pollen count. Most of the members of the Tertiary Component are represented in the woodland association, so it is likely that during this period of deposition the environment was more densely wooded, perhaps as a result of a milder climatic phase. This situation is more prominent at the Bee's Nest pit, where the whole assemblage represents the woodland association. Consequently the Tertiary Component here forms a higher percentage (67%) of the whole assemblage, due to the fact that this deposit is 7 Kms. to the south of Kenslow Top pit, and thus was further from the Neogene heath.

VI. AGE DETERMINATION

The fossil record from Neogene times shows that there are noticeable differences in the character of these assemblages and those from other provinces at similar latitudes, for example in different regions of Russia (Pokrovskaya, 1956) and Western North America (Wolfe, 1969). This is thought to be due to migration of the temperate flora from the Arctic south to most land masses in the present temperate regions. But due to the different events that occurred during migration, the temperate element in the N.W. European Neogene is different to that in other provinces (Leopold, 1970). There is sufficient similarity however, between the Derbyshire assemblage and those from deposits of similar age on the continent of N.W. Europe, to assume that all are part of the same floral province with a common origin.

Analysis of the major palynological assemblages that have been described from the Neogene of N.W. Europe shows that some taxa only survived in this region during that time. These forms, known as the European Neogene Component, were plants deduced to have migrated south as one province of the Arcto-Tertiary flora, and others that have remained in N.W. Europe throughout the Tertiary. Among both groups there were newly evolved taxa which are not present in Palaeogene floras either in N.W. Europe or in Arctic regions. It is the proportions of each taxa in any one assemblage that can give us clues to the age of that assemblage, if factors such as environment and location are taken into account. Comparison of palynological assemblages in the N.W. European province have enabled Zagwijn (1960), von der Brelie (1959) and others to designate various taxa to this Neogene Component. They were also able to divide this component into a Miocene Element and a Pliocene Element, as shown in Table 2. Von der Brelie has recently (1967) summarized the fossil record of some of the palynomorphs throughout the German Neogene, though slight variation in this can be expected for the European province as a whole, if only from the varying influence of the Alps and the Atlantic Ocean within this region.

Our understanding of the role of this Neogene Component seems to offer a reliable method for determining the age of European Miocene and Pliocene pollen assemblages. The present author has plotted the total number of elements within the Miocene and Pliocene Components (as listed in Table 2) from some of the better known European assemblages, against their approximate age. This curve is shown in Figure 7. The age determinations used in the curve are those of the investigator of the particular flora ; though in the case of floras of closely similar age, an accurate sequence along the x axis is not possible due to vertical deviation from the curves of up to about 10%.

This method leads to the conclusion that the Derbyshire assemblage is of a Miocene/Pliocene boundary age : an age rarely if ever, represented by non-marine deposits in N.W. Europe.

TABLE 2

Pollen taxa which have been cited (von der Brelie, 1959 ; Zagwijn, 1960) as members of the Pliocene and Miocene Components. Those marked with an asterisk are present in the Derbyshire assemblage.

PLIOCENE ELEMENTS	MIOCENE ELEMENTS
* *Pinus* haploxylon-type	*Engelhardtia* sp.
* *Sciadopitys* sp.	*Tricolpopollenites henrici*
* Taxodiaceae	* *T. microhenrici*
* *Tsuga* spp.	* *T. liblarensis*
* *Nyssa* sp.	*Cupuliferoipollenites villensis*
* *Liquidambar* sp.	*Tricolporopollenites pseudocingulum*
* *Carya* sp.	*T. cingulum*
Pterocarya sp.	*T. megaexactus brühlensis*
Castanea sp.	*T. euphorii*
Tricolpopollenites parmularius	*T. microreticulatus*
	* *T. edmundi*
	* *Symplocos* spp.

The individual taxa making up both the Miocene and Pliocene Components which are listed in Table 2 have their origins from two major sources. Either they are the products of the southerly migration from the Arcto-Tertiary flora, or else they have evolved from elements which occurred in N.W. Europe during the Palaeogene. A comparison of the living plant genera or those modern genera thought to have affinity with the pollen form species, listed in Table 2, with those present in the Palaeogene of southern England (Chandler, 1964) and the Arcto-Tertiary flora (Chaney, 1947 ; Takhtajan, 1969 ; Manum, 1962) shows that all genera were present within all three geofloras. This means that despite the presumed migrations up to and down from the Arctic, all the genera concerned remained distinct and changed in form only slightly (which we record as change in species). Within the limits of palynological identification to the modern generic level, it is possible to conclude that no major genus in the Neogene of N.W. Europe occurred in the Palaeogene Arcto-Tertiary flora without having representation at that same time in the warmer climates immediately to the south. This accords well with the views of Stebbins (1950, p. 526) that " since the beginning or end of the Eocene . . . in temperate regions few, if any, new genera have appeared ".

Since the Eocene then, plants in temperate climates are thought to have evolved only at the specific level, so that generic changes in the floras of these regions have been mainly due to migration. Both the Miocene and Pliocene Components in the Derbyshire assemblage represent separate definable waves of this migration process, which was brought about by the cooling climate. As this cooling became established, plants of the Miocene Component were the first to become extinct in this region

(Leopold (1968) used the term " extirpation " for this phenomenon), and were replaced by plants of the Pliocene Component which were presumably able to withstand slightly lower mean temperatures. These movements south have been recorded in southern France (Pons, 1964) where pollen of the N.W. European Miocene component is found in fairly large percentage frequency in deposits of roughly middle Pliocene age.

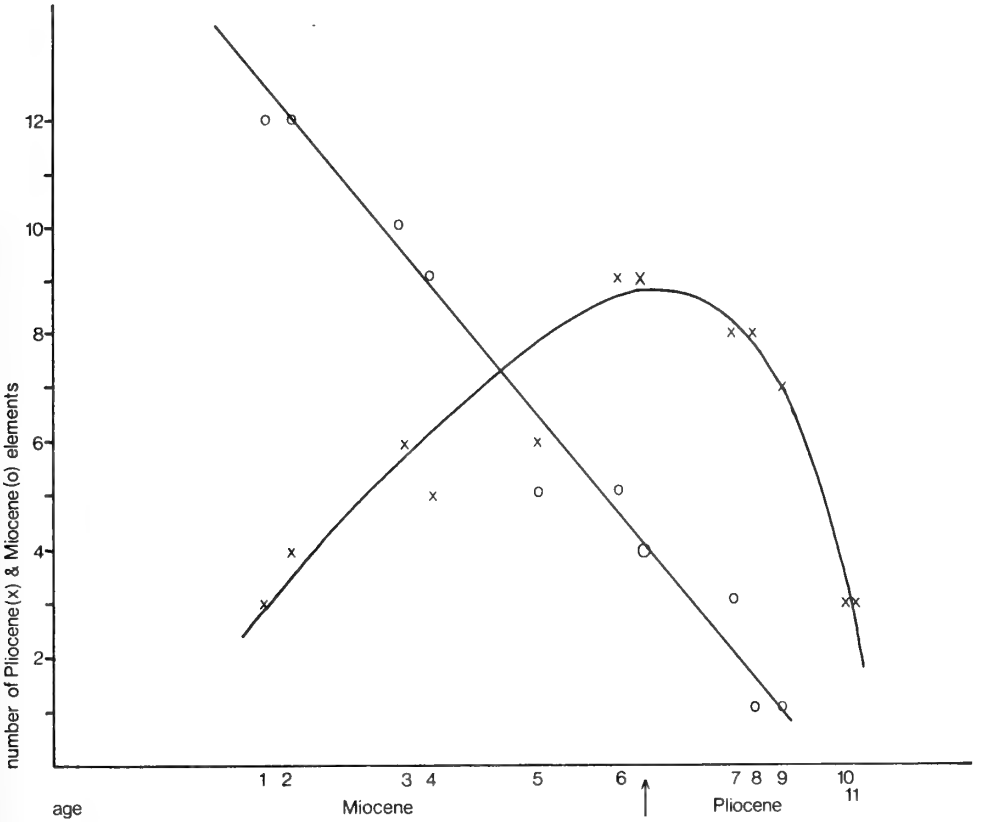

FIG. 7. Change in the number of Miocene (o) and Pliocene (x) Elements (see Table 2) present in eleven Neogene assemblages that have been described in the papers listed below. The numbers along the x axis refer to these eleven assemblages, though the sequence in which they are arranged along the axis is of little correlative significance, since the axis does not follow any accurate scale.

The arrow shows the age of the Derbyshire assemblage as determined by this method. 1. Upper Miocene. Neuy-Stolz, 1958. 2. Upper Miocene. Kremp, 1950. Steinberg no. 12. 3. Upper Miocene. Kremp, 1950. Delliehausen no. 6. 4. Upper Miocene. Pacltova, 1966. 5. Upper Miocene. Mazancova, 1962. 6. Branssumian. Zagwijn, 1967. Born 1 and 2. 7. Susterian. Zagwijn, 1960. Koningsbosch, Plate 9. 8. Upper Pliocene. Leschik, 1951. Flöz 1. 9. Reuverian. Altehenger, 1959. Wallensen (K). 10. Reuverian. Zagwijn, 1960. Susterian Diagram, Plate 11. 11. Tiglian. Zagwijn, 1963. Tegelen Diagram.

The precise destiny of this Neogene Component after the end of the Pliocene is not clear. Many of its elements, such as *Carya, Tsuga,* and the Taxodiaceae are now only native to very restricted regions of N. America and E. Asia : regions upon which the N.W. European Component can have had no direct influence. This suggests that by the end of the Early Pleistocene many species of the Component became extinct in N.W. Europe ; perhaps their routes of migration were blocked by the Alps and the Mediterranean (Takhtajan, 1969, p. 204) but there is no direct fossil evidence for this.

The possible complete extinction of most members of the N.W. European Neogene Component reinforces the argument that has been used several times in the systematic part of this paper that its species are dissimilar from any living today. The two species of *Tsuga* represented in the pollen of the Derbyshire assemblage (and which occur abundantly in Neogene deposits throughout Europe) are unlikely to have had any contact with the living *Tsuga canadensis* or *T. diversifolia* since the time of the Arcto-Tertiary flora. Since then, the Atlantic Ocean isolated the North American species from other members of the genus in S.E. Asia and Neogene Europe. Had *T. diversifolia* stretched right across Eurasia during the Neogene, surely the species would now occur in the Near East (as for instance does *Cedrus lebani* ; this genus is represented in the Derbyshire Neogene) or say in the southern part of Asia. The occurrence in N.W. Europe during the Neogene, of genera that are now isolated by both the Atlantic and Europe are more likely to have migrated from a point of common origin in the north than to have had originally a continuous wide distribution. The European Neogene would have been a third area that the same genera colonized during this time, very likely as distinct species that are now extinct.

VII. THE NEOGENE ENVIRONMENT IN DERBYSHIRE

The distribution of the fossil plants as well as the nature of the clay itself, has led to the conclusion that the material of the plant bed has been deposited subaqueously. The underlying sands and clays also show evidence that they have been deposited under similar conditions, perhaps as a result of more rapid flow, since signs of current bedding are preserved in parts of the sand deposit at Kenslow Top pit. The present limestone surface in which the sink hole deposits occur forms what Linton (1956) has called the Peak District Upland Surface, and this, during late Tertiary times (as now) lay to the south of the much higher Holme Moss Surface (Sissons, 1954) of Millstone Grit. So it seems acceptable to suppose that the Holme Moss Surface of Neogene times provided the source of fluvial activity which gave rise to some of the sands and clays which are found today in the sink hole deposits. The only direct evidence for this within the sink hole deposits themselves (apart from the current bedding features) can be found at the most basal part of the Kenslow Top pit plant bed. In the clay at this part of the bed (which is below the section shown in Figure 6), reworked Namurian miospores (Neves, 1958) form a significant part of the assemblage ; they do not occur at all however in the major part of the plant bed, nor in any other of the deposit's sands and clays. Indeed, the sands and pebbles of the pocket

deposits are thought to be dominantly derived from the retreating Triassic scarp to the south (Ford & King, 1968).

Current geomorphological theory suggests that during Oligo-Miocene times, Pennine uplift caused the Derbyshire limestone to assume a significant height above sea level (Linton, 1956). It may have been as a result of these movements that a river system from the higher Holme Moss Surface became well established, and that deposition of the plant bed subsequently occurred.

Analysis of the fossil plants present in the Derbyshire assemblage does not help very much in determining the exact nature of the fluviatile process that is thought to have been concerned with deposition. The only aquatic (or swampy) forms present in the pollen assemblage (in very small quantities) are *Taxodium*-type and *Nyssa* sp., both of which are difficult to assign either to modern species of known ecological character, or to other fossil types which have been described from deposits of freshwater origin (e.g. Szafer, 1954). This scarcity suggests that the pollen-bearing clay was deposited by either a slowly moving river or else by the reworking of Neogene sediment of unknown form which might have occurred around the collapsed sink hole (see Section V, page 396). The two plant associations that have been identified from the quantitative analysis of samples from Kenslow Top pit can be interpreted as occupying separate parts of the Neogene surface in Derbyshire ; the Ericaceous heathland for instance on the higher and more northerly (and therefore more distant point from Bee's Nest pit, where the association is poorly represented) Holme Moss Surface, whilst the woodland association occupied the intermediate neighbourhood near the deposits themselves. But the structure of the Neogene vegetation could have been more complex than this, as will be appreciated by comparison to the modern vegetation patterns of the region today. The Neogene environment is likely to have been simpler than the modern one, due to the absence then of glacial till and the existence of a younger landscape, but local niches could have existed for example possibly on exposed dolomite tors (it is debatable if these were exposed during the Neogene) or in river valleys. Although such niches are of common occurrence in temperate zones, they are absent in most tropical regions (Van Steenis, 1969) and so may have been less common than now in Neogene Derbyshire. Further ecological analysis or comparison of the members of the Derbyshire assemblage with modern plant associations is severely limited by the uncertain specific affinities of most of the important fossil types. There is similar difficulty involved with the deduction (or rather, induction) of climatic influences from the modern genera that we believe to have been present in the Derbyshire Neogene environment. For instance, genera such as *Hedera* and *Ilex* that are regarded as characteristic inhabitants of oceanic climates in Europe today, may have existed during the Neogene as species with different climatic demands. But since different genera even of the same ecological affinity are thought to have evolved at quite different rates (Stebbins, 1950, p. 551 et seq.), climatic trends can be most accurately estimated by considering groups of plants rather than individual genera. It has become general practice for ecologists to separate elements of the modern British flora into various climatically distinct geographical elements (Matthews, 1937), based on their current areas of distribution, not their centre of origin. A similar system has recently been devised for Tertiary

floras by Krutzsch & Majewsky (1967), who separated widely distributed European Neogene palynomorphs into four groups : warm, intermediate, temperate and facies elements. Most members of the first two of these divisions are now extinct in Europe, whilst members of the Tertiary Component (see Section V) are represented in all four groups. The assignments are based on the present climatic requirements of the modern genera with presumed affinity to the fossil forms, and so in some cases may not be correct. On the basis of this work, the Derbyshire assemblage has been separated into climatic divisions which are shown in Table 3.

TABLE 3

Climatic groups of some members of the Derbyshire assemblage, after Krutzsch & Majewsky (1967).

WARM ELEMENT	INTERMEDIATE ELEMENT	TEMPERATE ELEMENT	FACIES ELEMENT
Verrucatosporites favus	*Keteleeria*	*Tsuga*	*Pinus*
Leiotriletes	*Abies*	*Neogenisporis*	*Nyssa*
Podocarpus?	*Cedrus*	Polypodiaceae	*Alnus*
Sapotaceae	quercoid types	*Picea*	*Ilex*
T. *edmundi*	*Juglans*	*Sciadopitys*	Taxodiaceae
Hedera sp.	*Carya*	*Ulmus*	Ericaceae
Symplocaceae		*Liquidambar*	Sphagnaceae
		Corsinipollenites	
		Carpinus	
		Corylus	
		Compositae	
		Graminae	

The modern British flora is distinguished from that of the European continent by the effects of a temperate oceanic climate. West (1961) has suggested that high oceanicity was prevalent during the Early Pleistocene too, encouraging the development of *Empetrum* heathland which had many of the temperate genera that are found in the Derbyshire heathland association. West's comparison of the British Early Pleistocene flora to those of the Netherlands and southern Poland led him to the conclusion that the gradient of oceanicity/continentality of climate across Europe was probably more marked than that at present. At the beginning of the Pliocene however, western and central European floras showed no significant difference either of a qualitative or quantitative type ; genera such as *Tsuga, Empetrum, Rhododendron, Hedera* and *Ilex* which have modern species characteristic of oceanic climate are widely distributed into Central Europe during the Neogene (see for example, Pacltova's (1966) description of the Kovacova flora from southern Slovakia). There are two possible explanations to account for this apparently wide distribution: either the oceanic species cannot be recognized palynologically, or else the warm climate in Europe during the Neogene did not produce the same kind of gradient across the continent that exists today.

VIII. ACKNOWLEDGMENTS

I would like to thank Dr. P. Walsh and Dr. T. Ford for advice on the geomorphological aspects of this work, and Dr. B. Pacltova for her help with many of the palynological identifications. It was from her also that I acquired much of my comparative material of the European Neogene. A grant from the British Council enabled me to work on this project in Czechoslovakia, and West Ham College of Technology generously supplied me with money for the borehole through the Friden plant bed.

Throughout the whole project, my supervisor Dr. W. G. Chaloner has given much of his time and ingenuity to the work. I am immeasurably indebted to him for this help, and for his enthusiastic inspiration.

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N.E. LONDON POLYTECHNIC,
LONDON, E.15

PLATE 1

All magnifications × 1,000

FIG. 1. *Stereisporites* (*St.*) *stereoides stereoides* (R. Pot. & Ven.) Th. & Pf. V.55658
FIGS. 2 a, b. *S.* (*St.*) *minor microstereis* Kr. V.55652
FIG. 3. *S.* (*Distanc.*) *crucis* Kr. V.55652
FIGS. 4 a, b. *S.* (*Distanc.*) *wehningensis* Kr. V.55653
FIGS. 5 a, b, c. *S.* (*Distanc.*) *germanicus rhenanus* Kr. V.55666
FIG. 6. *S.* (*Distverrus.*) *pliocenicus pliocenicus* Kr. V.55634
FIGS. 7 a, b. *S.* (*Distgranisp.*) *granisteroides* Kr. V.55658
FIGS. 8 a, b. *S.* (*Distgranisp.*) *minimoides* Kr. V.55652
FIGS. 9 a, b. *S.* (*Stereigranisp.*) *semigranulus* Kr. V.55663
FIGS. 10 a, b. *S.* (*Stereigranisp.*) *magnoides* Kr. V.55658
FIGS. 11 a, b. *S.* (*Distzono.*) *microzonales* Kr. V.55631

All the specimens figured here are registered and deposited in the collections at the British Museum (Natural History).

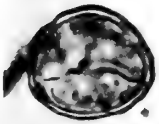
1

3

4a

4b

2a

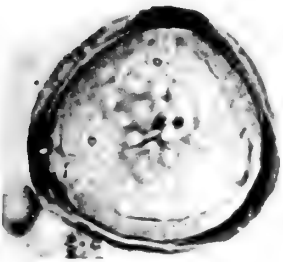


2b

5a

5b

5c



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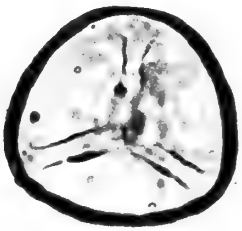

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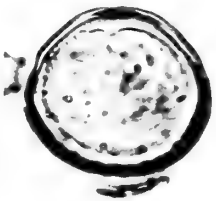


8b

9a

9b

10a

10b

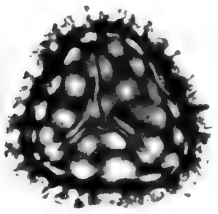
11a

11b

PLATE 2

All magnifications × 1,000

Figs. 1 a, b.	*Lycopodium* sp. V.55644
Figs. 2 a, b, c.	*Gleicheniidites senonicus* Ross, emended Skarby. V.55650
Figs. 3 a, b.	*Osmunda* sp. V.55634
Figs. 4 a, b.	*Verrucatosporites favus* (R. Pot.) Th. & Pf. V.55665
Figs. 5–6.	*Laevigatosporites haardti* (R. Pot. & Ven) Th. & Pf. V.55650
Figs. 7 a, b.	*Leiotriletes wolffi wolffi* Kr. V.55649
Fig. 8.	*L. wolffi brevis* Kr. V.55652
Fig. 9.	*Triplanosporites microsinuosus* Kr. V.55647



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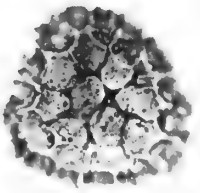

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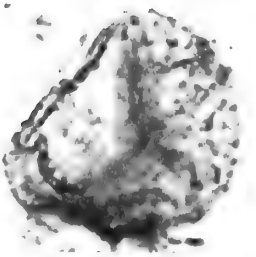
3a



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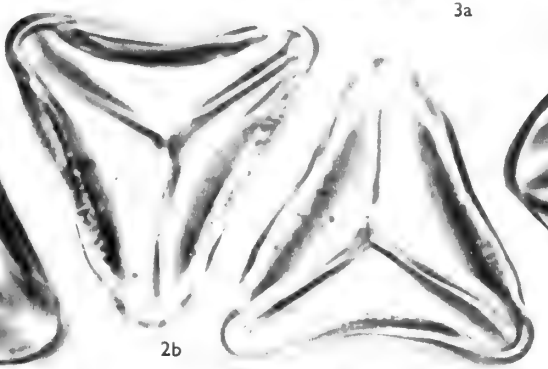

2b

7a

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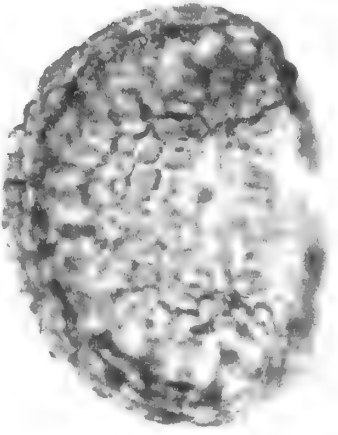
7b

4a



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8

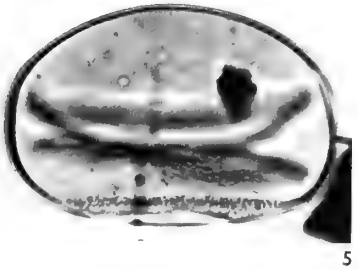

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PLATE 3

FIG. 1. *Inaperturopollenites hiatus* (R. Pot.) Th. & Pf., × 1,000 V.55655
FIG. 2. *I. dubius* (R. Pot.) Th. & Pf., × 1,000. V.55633
FIG. 3. *Cryptomeria* sp., × 1,000. V.55632
FIG. 4. *Sciadopitys* sp., × 1,000. V.55630
FIG. 5. *Abies* sp., × 500. V.55634
FIGS. 6 a, b. *Cedrus* sp., × 1,000. V.55634
FIG. 7. *Keteleeria* sp., × 500. V.55657

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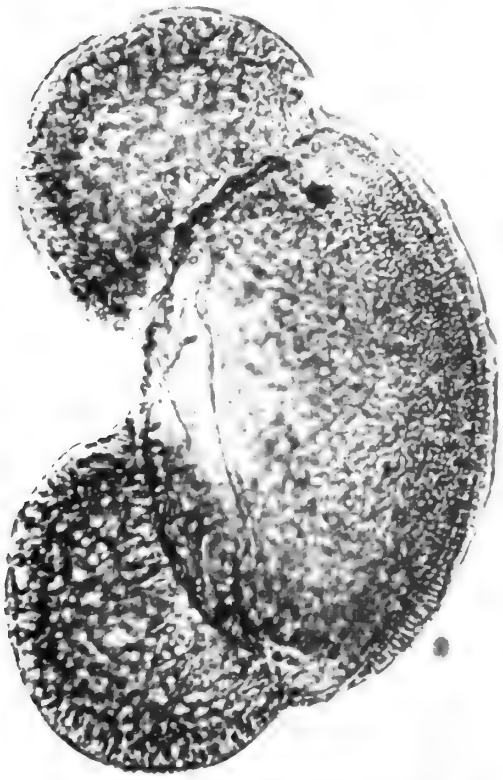

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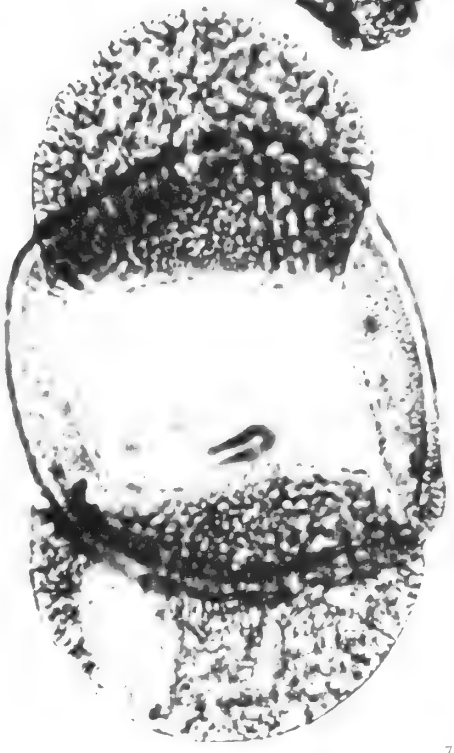

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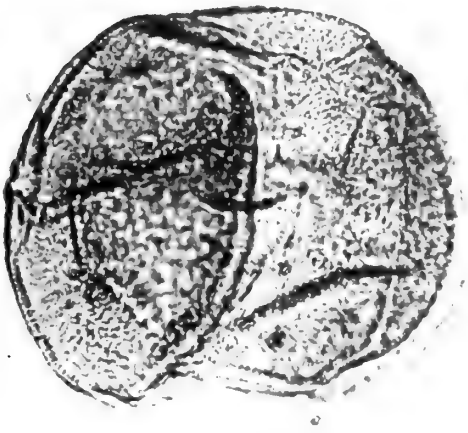
6a

6b

PLATE 4

All magnifications × 1,000

FIGS. 1 a, b. *Picea* sp. V.55634
FIGS. 2 a, b. *Pinus* sylvestris-type. V.55640
FIGS. 3 a, b. *Pinus* sylvestris-type. V.55634



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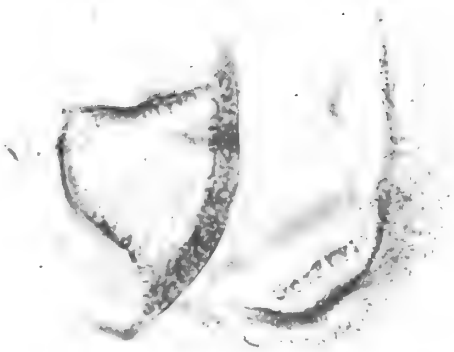

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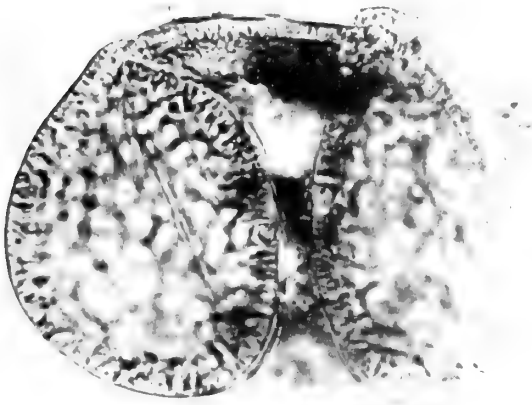

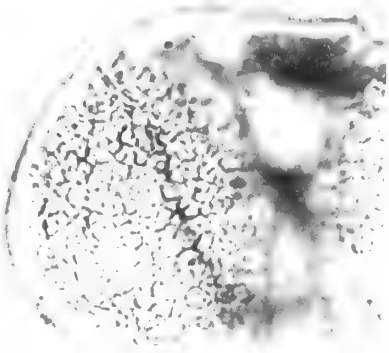

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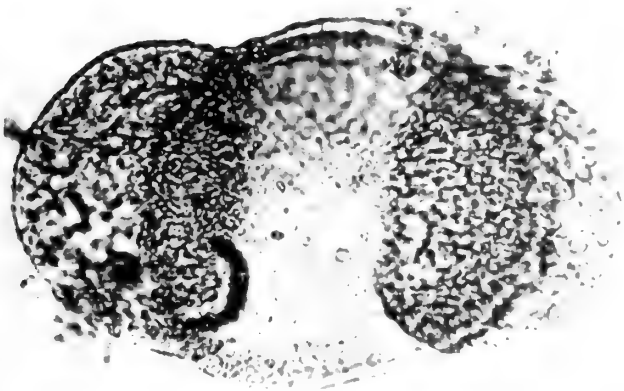
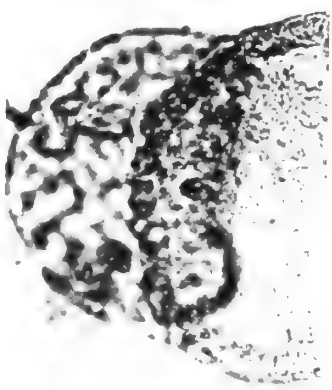




3a 3b

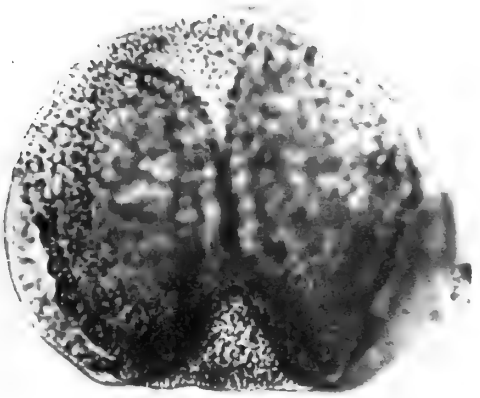
PLATE 5

All magnifications × 1,000

FIG. 1. *Pinus* sylvestris-type. V.55634

FIGS. 2–5. *Pinus* haploxylon-type. V.55636 ; V.55634 ; V.55635

PLATE 5



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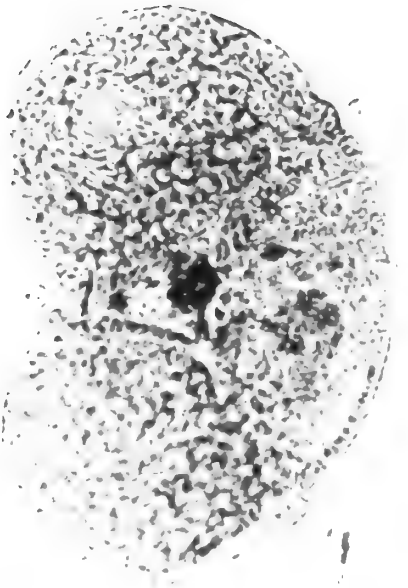

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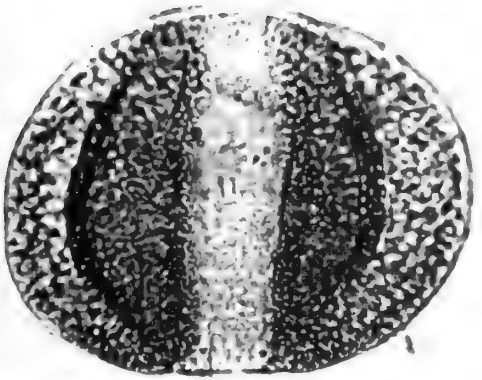

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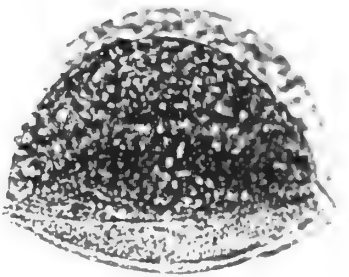

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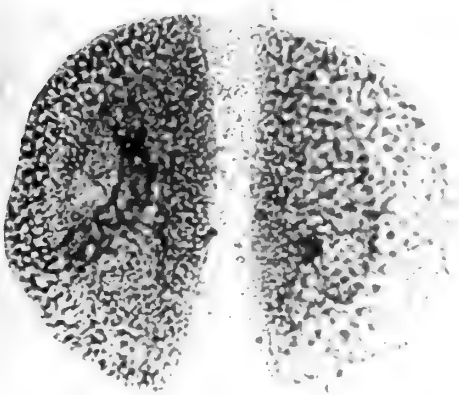

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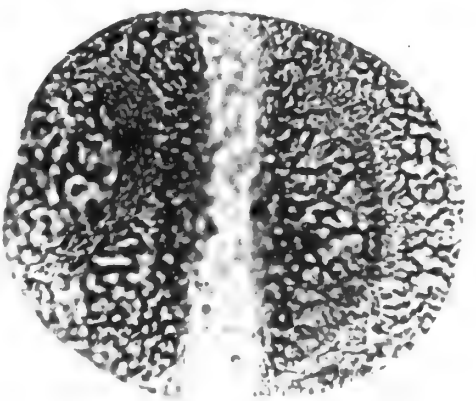
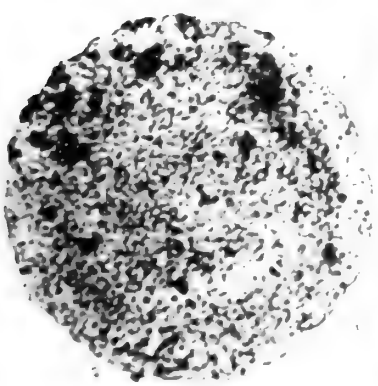


5b

PLATE 6

FIG. 1 a. *Tsuga* canadensis-type, × 500. V.55639
FIG. 1 b. *T.* canadensis-type, × 2,000. V.55639
FIG. 2. *T.* diversifolia-type, × 1,000. V.55641
FIGS. 3–4. *Podocarpoidites libellus* R. Pot. × 1,000. V.55634 ; V.55637



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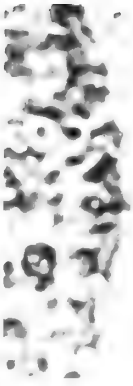

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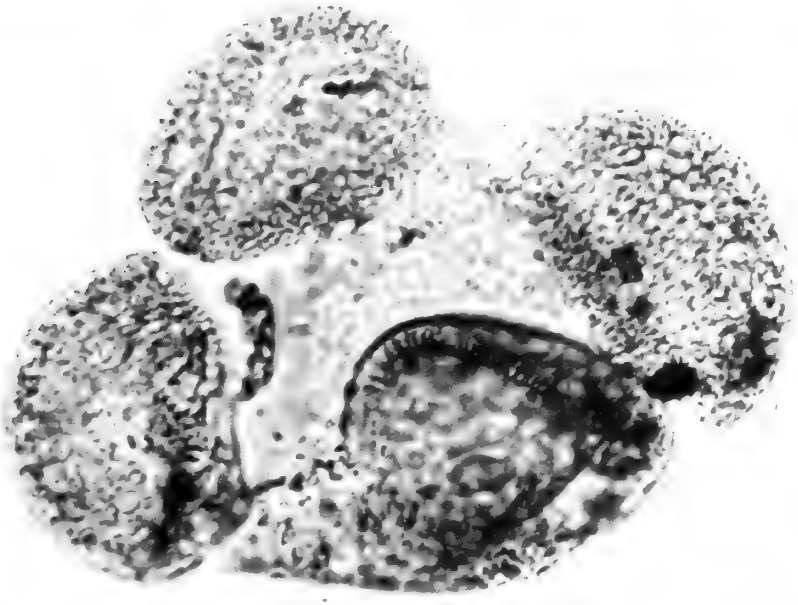

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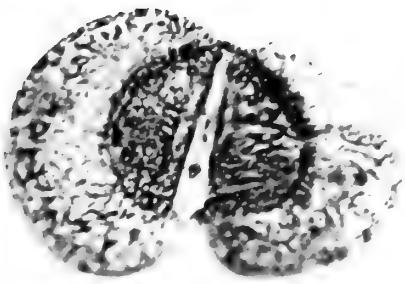

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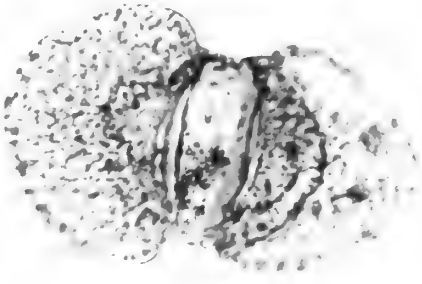
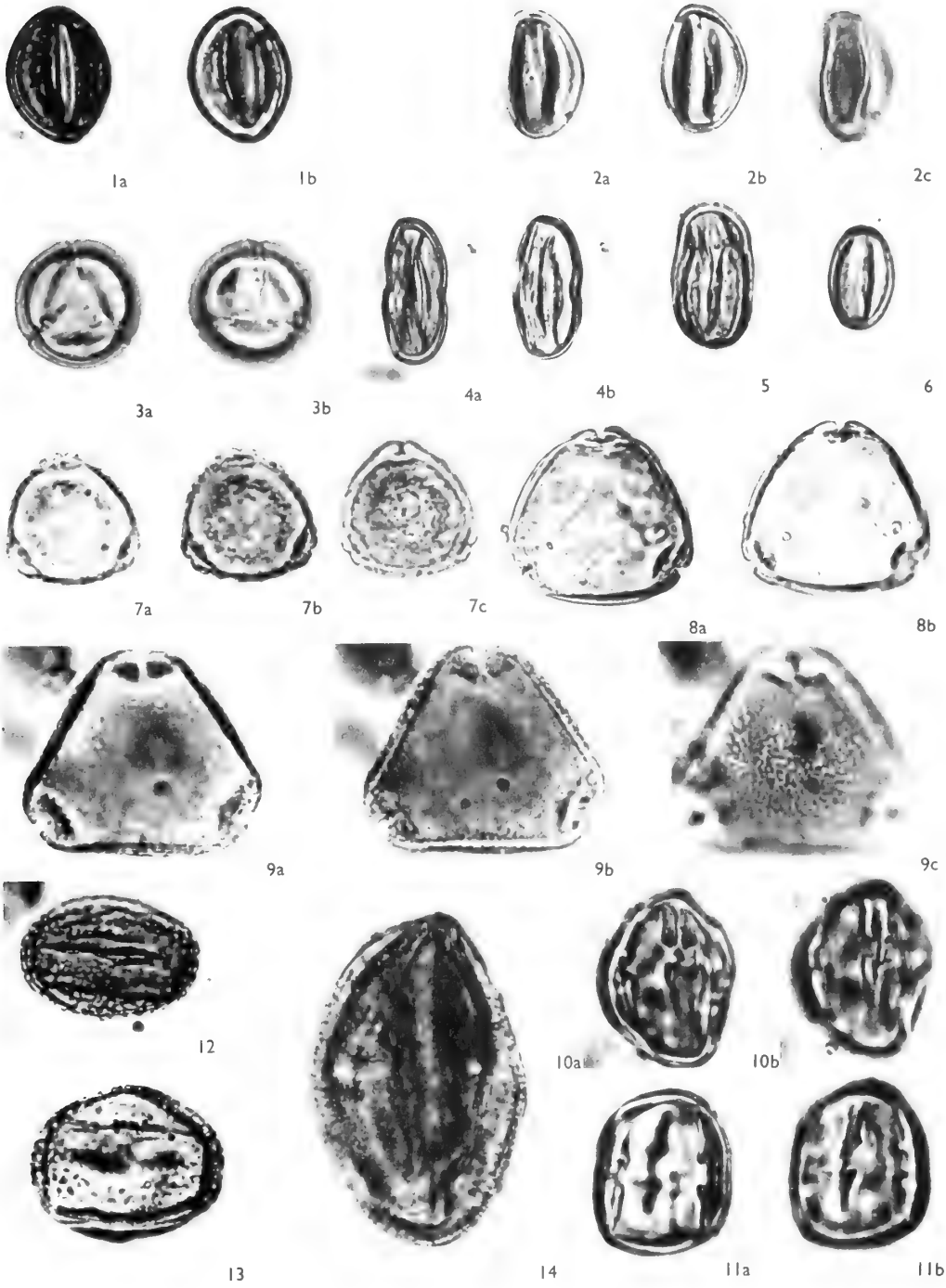


4b

PLATE 7

All magnifications × 1,000

FIGS. 1–3.	*Tricolpopollenites ipilensis* Paclt. V.55639 ; V.55638
FIGS. 4–5.	*T. liblarensis liblarensis* (Th.) Th. & Pf. V.55651 ; V.55634
FIG. 6.	*T. liblarensis fallax* (R. Pot.) Th. & Pf. V.55649
FIGS. 7 a, b, c.	*Porocolpopollenites vestibulum* (R. Pot.) Th. & Pf. V.55650
FIGS. 8 a, b.	*P. rotundus* (R. Pot.) Th. & Pf. V.55660
FIGS. 9 a, b, c.	*P. vestibulum* (R. Pot.) Th. & Pf. V.55650
FIGS. 10–11.	*Nyssa* sp. V.55660
FIGS. 12–13.	*Hedera* sp. V.55652 ; V.55660
FIG. 14.	*Tricolporopollenites edmundi* (R. Pot.) Th. & Pf. V.55634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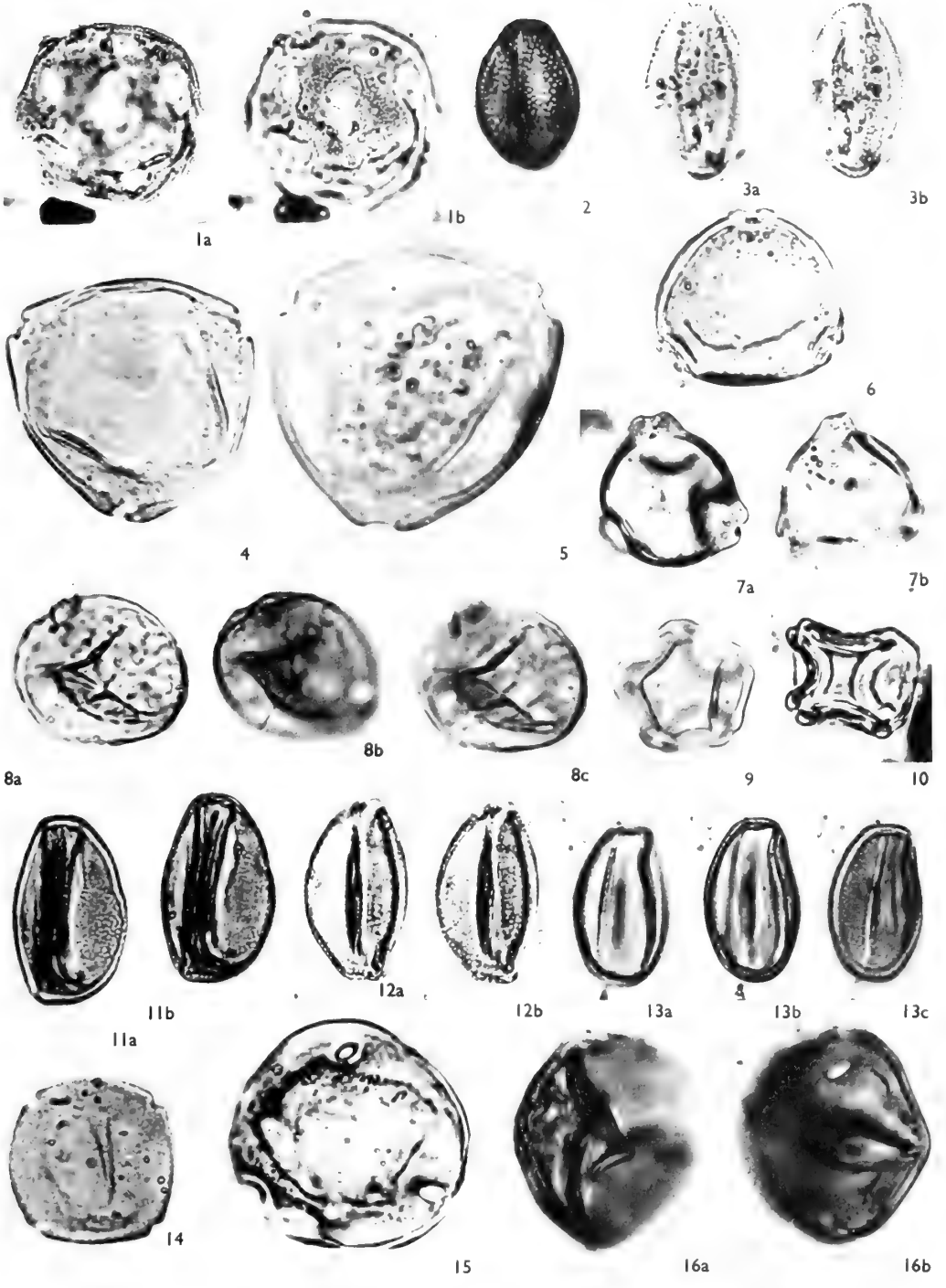
10b
13
14
11a
11b

PLATE 8

All magnifications × 1,000

FIGS. 1 a, b. *Liquidambar* sp. V.55660
FIG. 2. *Salix* sp. V.55635
FIGS. 3 a, b. *Tricolpopollenites retiformis* Th. & Pf. V.55639
FIG. 4. *Myrica* sp. V.55643
FIG. 5. *Corylus* sp. V.55662
FIGS. 6–7. *Trivestibulopollenites betuloides* Th. & Pf. V.55642 ; V.55664
FIGS. 8 a, b, c. *Ulmus* sp. V.55634
FIGS. 9–10. *Alnus* sp. V.55648 ; V.55659
FIGS. 11–13. *Tricolpopollenites microhenrici* (R. Pot.) Th. & Pf. V.55634 ; V.55635 ; V.55639
FIG. 14. *Carpinus* sp. V.55653
FIG. 15. *Carya* sp. V.55634
FIGS. 16 a, b. *Juglans* sp. V.55634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13b
13c
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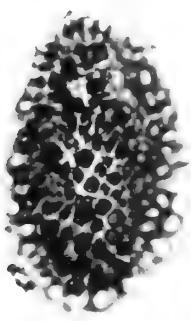
16a
16b

PLATE 9

All magnifications × 1,000

Figs. 1 a, b.	*Tricolporopollenites iliacus* (R. Pot.) Th. & Pf. V.55649
Figs. 2 a, b.	*T. margaritatus* (R. Pot.) Th. & Pf. V.55654
Figs. 3 a, b, c.	*Tetracolporopollenites sapotoides* Th. & Pf. V.55661
Fig. 4.	*Compositoipollenites rizophorus* R. Pot. V.55654
Fig. 5.	*Corsinipollenites maii* Kr. V.55656
Figs. 6 a, b.	*Periporopollenites echinatus* (Wode.) Th. & Pf. V.55660
Figs. 7–8.	*Empetrum* sp. V.55645 ; V.55646
Fig. 9.	*Calluna* sp. V.55635
Fig. 10.	? *Rhododendron* sp. V.55660
Figs. 11 a, b.	? *Erica* sp. V.55656
Figs. 12–13.	*Graminidites media* Cookson. V.55661 ; V.55652



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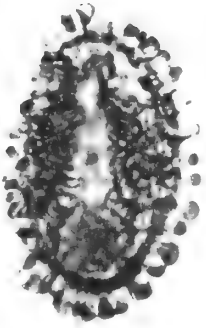

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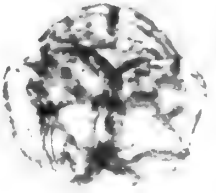

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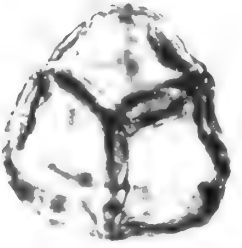

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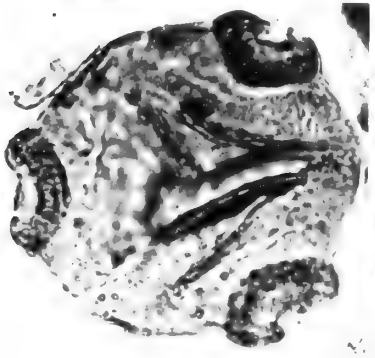

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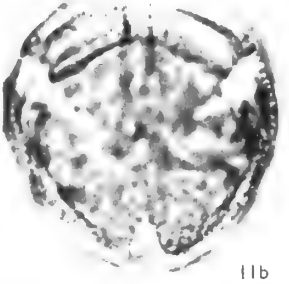

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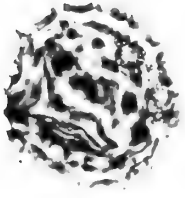

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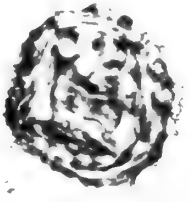

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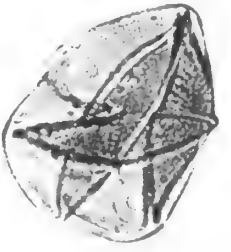

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THE LOWER PALAEOZOIC STRATIGRAPHY AND FAUNAS OF THE TAURUS MOUNTAINS NEAR BEYŞEHİR, TURKEY. I. STRATIGRAPHY

BRITISH MUSEUM
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NATURAL HIST

W. T. DEAN
AND
O. MONOD

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 19 No. 8
LONDON: 1970

THE LOWER PALAEOZOIC STRATIGRAPHY AND FAUNAS OF THE TAURUS MOUNTAINS NEAR BEYŞEHİR, TURKEY.

I. STRATIGRAPHY

BY

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Pp. 411–426 ; 8 *Text-figures*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

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World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.).

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 24 *December*, 1970 *Price* 65p.

THE LOWER PALAEOZOIC STRATIGRAPHY AND FAUNAS OF THE TAURUS MOUNTAINS NEAR BEYŞEHİR, TURKEY.

I. STRATIGRAPHY

By W. T. DEAN & O. MONOD

CONTENTS

		Page
I.	Introduction and acknowledgments	413
II.	Cambrian rocks : The Çal Tepe formation	416
III.	Ordovician rocks : Seydişehir formation & Sobova formation	419
	(a) Seydişehir Shales & Upper Greywackes	419
	(b) Sobova Limestone & overlying strata	422
IV.	Summary of conclusions	424
V.	References	426

SYNOPSIS

The Lower Palaeozoic strata of the Beyşehir region, south-west of Konya, are described. The Cambrian rocks are well developed as the Çal Tepe Formation, at least 130 metres thick and divisible into four parts. The lowest two subdivisions consist of unfossiliferous dolomite and unfossiliferous black limestone respectively. The third part comprises light-grey limestones which contain trilobites of both Lower(?) and Middle Cambrian age. The highest beds contain Middle Cambrian trilobites and are succeeded by the shales of the Seydişehir Formation, Ordovician at least in part. The succession exhibiting the junction of the two systems is overturned on the Çal Tepe itself and the neighbouring hills. Large outcrops of the Seydişehir Shales have yielded small numbers of trilobites, graptolites, brachiopods and molluscs which indicate an Arenig age for the upper half of the Seydişehir Formation and exhibit affinities with other faunas of Tethyan type in the Mediterranean region. The Seydişehir Shales are succeeded by a small thickness of " Upper Greywackes ", followed in turn by the Sobova Formation. The latter is best developed, as limestones, in the Sobova Valley, south of Beyşehir, and contains a trilobite fauna of Arenig age in which predominantly Baltic elements occur, together with a minority of Tethyan forms. Grey shales, also of Arenig age, immediately above the Sobova Limestone at its type locality, pass laterally into red sandstones at Taraşçı, and both are overlain unconformably by limestones of Triassic or Jurassic age.

I. INTRODUCTION AND ACKNOWLEDGMENTS

The Taurus mountain range stands between the plateau of Central Anatolia, to the north, and the Mediterranean Sea, to the south. It extends eastwards from the southern Aegean coast of Turkey to northern Iran, and its overall width varies considerably. Most of the mountains which make up the Taurus are composed of Mesozoic formations, but an older substratum of Palaeozoic rocks appears occasionally, mainly along the northern border of the range. North of the region around

Beyşehir, about 100 kilometres southwest of Konya (see Fig. 1), the Taurus runs south-southeastwards along the southern margin of an older Palaeozoic massif, the Sultan Dağ, the rocks of which have been metamorphosed and strongly deformed tectonically. The geology of part of the Sultan Dağ was described by both H. Haude and D. Kelter in unpublished theses of the University of Münster, the contents of which have recently been summarized by Haude (1969). Prior to the discovery of

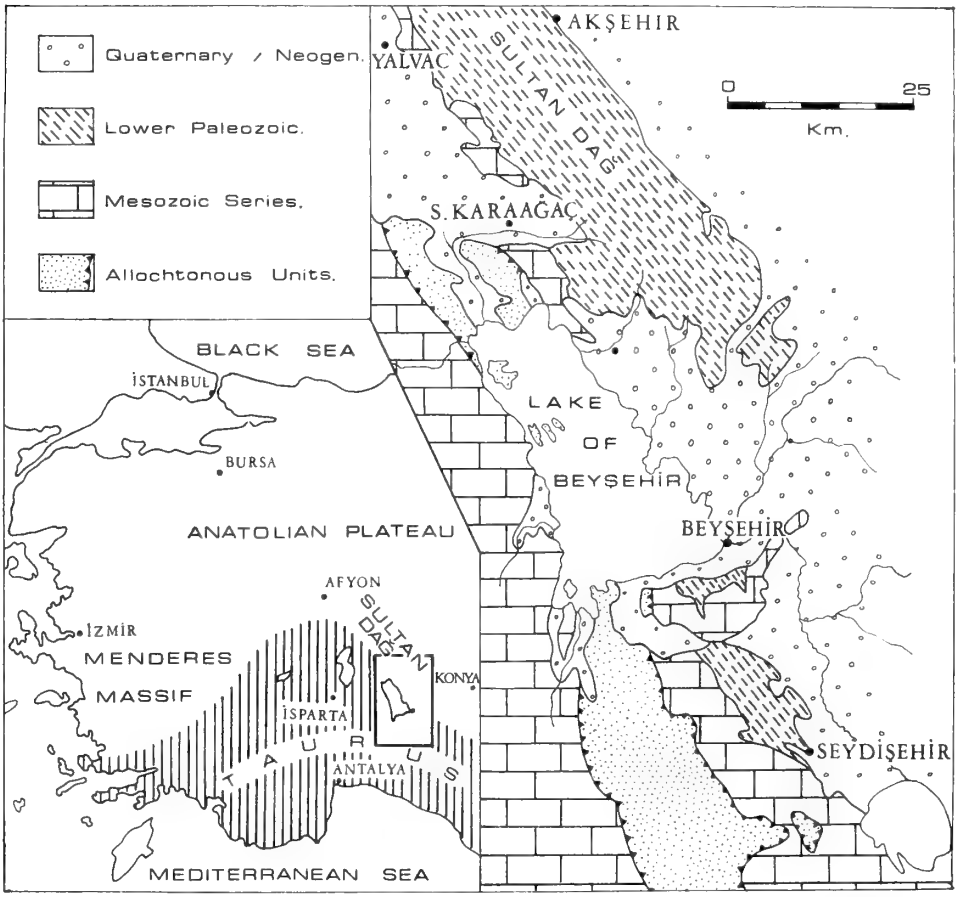

FIG. 1. Geological sketch-map showing the location of the area investigated in the western Taurus Mountains. Modified from the Konya Sheet of the 1 : 500,000 geological map of Turkey.

Cambrian rocks in the Beyşehir region Kelter and Haude had found Middle Cambrian fossils on the Sultan Dağ, and this information proved useful in the search for fossiliferous horizons on Çal Tepe.

South of Beyşehir, large outcrops of some of the older formations of the Sultan Dağ occur, but in this region the rocks are less disturbed tectonically and numerous

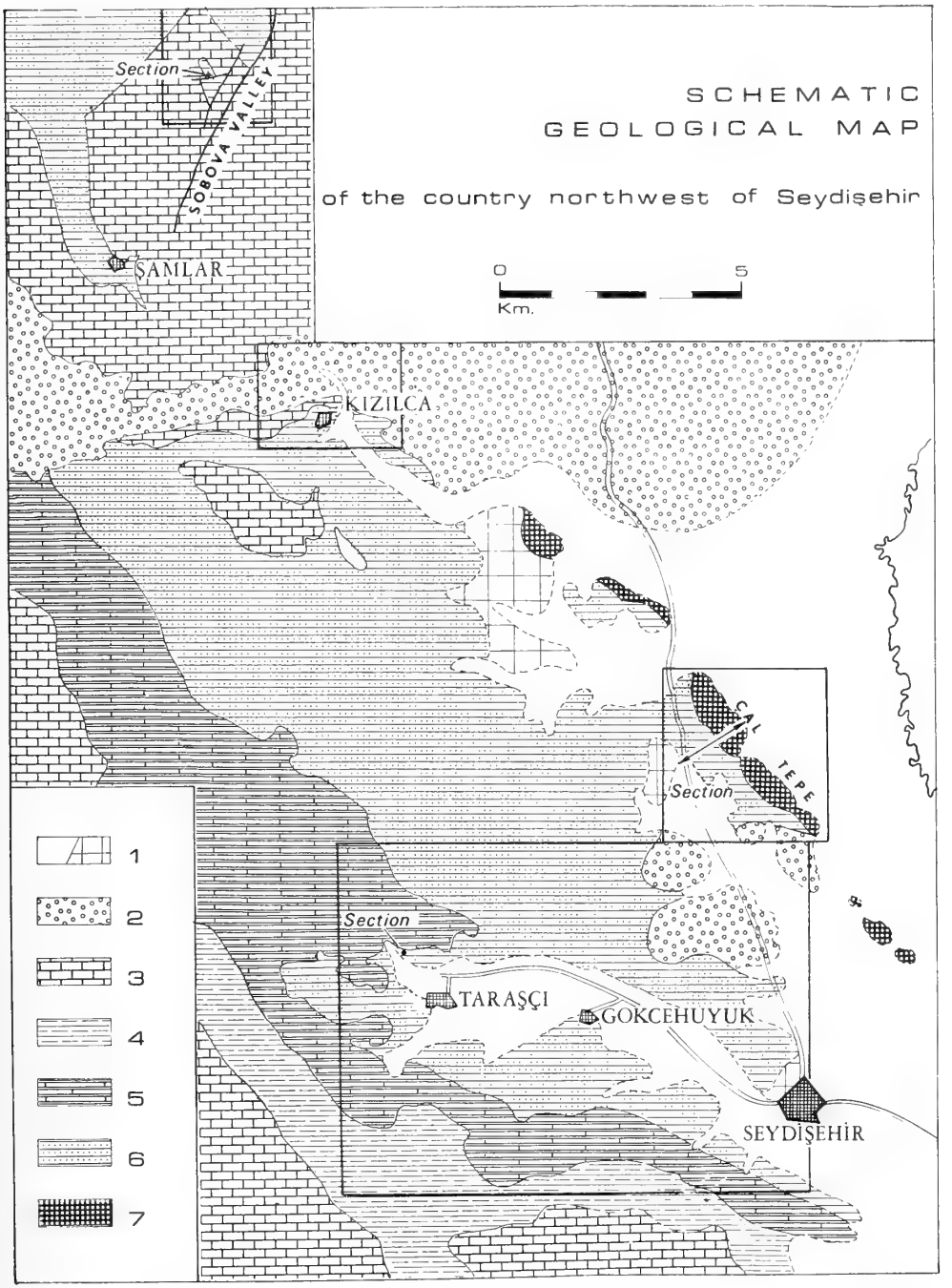

FIG. 2. Schematic geological map of the country northwest of Seydişehir. Geological boundaries by O. Monod. 1 = Recent deposits and Quaternary travertine ; 2 = Upper Neogene conglomerates and marls ; 3 = Jurassic and Cretaceous limestones ; 4 = Şarpiar Formation (Upper Trias—Lias ?) ; 5 = Taraşçı Limestones (Middle Trias) ; 6 = Seydişehir Formation (Lower Ordovician in part) ; 7 = Çal Tepe Formation (Lower ?—Middle Cambrian). Rectangles show position of areas in Figs. 3, 5 and 6.

fossiliferous localities have been found. Publications describing the geology of the region are few. Blumenthal, in a remarkable paper of 1947, provided the first geological map. He introduced the stratigraphical term Seydişehir Shales (as Seydişehir-Schiefer) and, without finding fossil evidence for their age, assigned these strata to the Devonian. The Seydişehir Shales (at least in part) are here put in the Lower Ordovician. Blumenthal believed that the calcareous strata now called the Çal Tepe Formation, of Cambrian age, were interbedded within the Seydişehir Shales, a not unreasonable suggestion, since it was not then appreciated that the Cambro-Ordovician succession at Çal Tepe itself is inverted (see Fig. 4). Since 1965 O. Monod has been engaged in the geological mapping of the Beyşehir–Seydişehir region of the Taurus, thanks to an agreement with the Maden Tetkik ve Arama Enstitüsü (M.T.A.) at Ankara. In the course of this work several fossiliferous localities were discovered in the old substratum of the Taurus and proved to be of Cambrian and Ordovician age. The fossils are mostly trilobites, indentified by W. T. Dean, but some graptolites, cephalopods and brachiopods were found, and we are indebted to Drs. P. Toghill, D. H. Collins, H. Brunton and L. R. M. Cocks for their identification. Some of the earlier discoveries were described by Monod (1967) in a paper which demonstrated the Ordovician age of the Seydişehir Shales for the first time. Early in the summer of 1968 O. Monod and W. T. Dean together made additional collections, mostly of trilobites which will be described at a later date, and the fauna of the Sobova Limestone was discovered. The purpose of the present paper is to establish the Cambrian and Ordovician stratigraphy of the region and, as far as possible, the stratigraphical position of the principal fossil localities. Prof. H. B. Whittington kindly read the manuscript and made useful suggestions for its improvement.

II. CAMBRIAN ROCKS: ÇAL TEPE FORMATION

The rocks of this formation are the oldest seen in the region, and form a conspicuous line of hills some 10 kilometres north of Seydişehir and near the road to Beyşehir. The hills extend approximately northwestwards in the direction of strike.

The largest hill, known as the Çal Tepe (or İdisçal Tepe *in* Blumenthal, 1947) exhibits good exposures and the section near its southeastern end is taken as type for the Çal Tepe Formation, even though the succession there is overturned (see Fig. 4). The Cambrian outcrop here is bounded on the southwest by the Seydişehir Shales, and on the northeast by superficial deposits of Quaternary to Recent age. The term Çal Tepe Formation is used to include the whole of the Cambrian carbonate rock succession at this point, which may be subdivided as follows :—

Çal Tepe Formation	Çal Tepe Limestone	U	Bed d. Thinly-bedded red nodular limestone with grey limestone bed (less than 1 metre thick) at top	Up to 40 m.
		L	Bed c. Light-grey limestone	Approx. 10 m.
			Bed b. Black, massively-bedded limestone	30 m.
	Çal Tepe Dolomite	——	Bed a. Massively-bedded, coarsely-crystalline dolomite	more than 50 m.

Bed a. forms the lower part of the northeastern flank of Çal Tepe, and is fairly well

exposed there. The rocks, which have not yielded any traces of fossils, are at least 50 metres thick and the stratigraphical base has not been seen, the outcrop being terminated by Quaternary to Recent deposits. The dolomite may be traced south-eastwards along the strike to the neighbouring, smaller hill of Guvercin Tepe and the still smaller hill beyond (see Fig. 3).

Bed b. is a massive, black, crystalline limestone which forms a conspicuous small cliff along the crest of Çal Tepe and Guvercin Tepe. No traces of fossils were found.

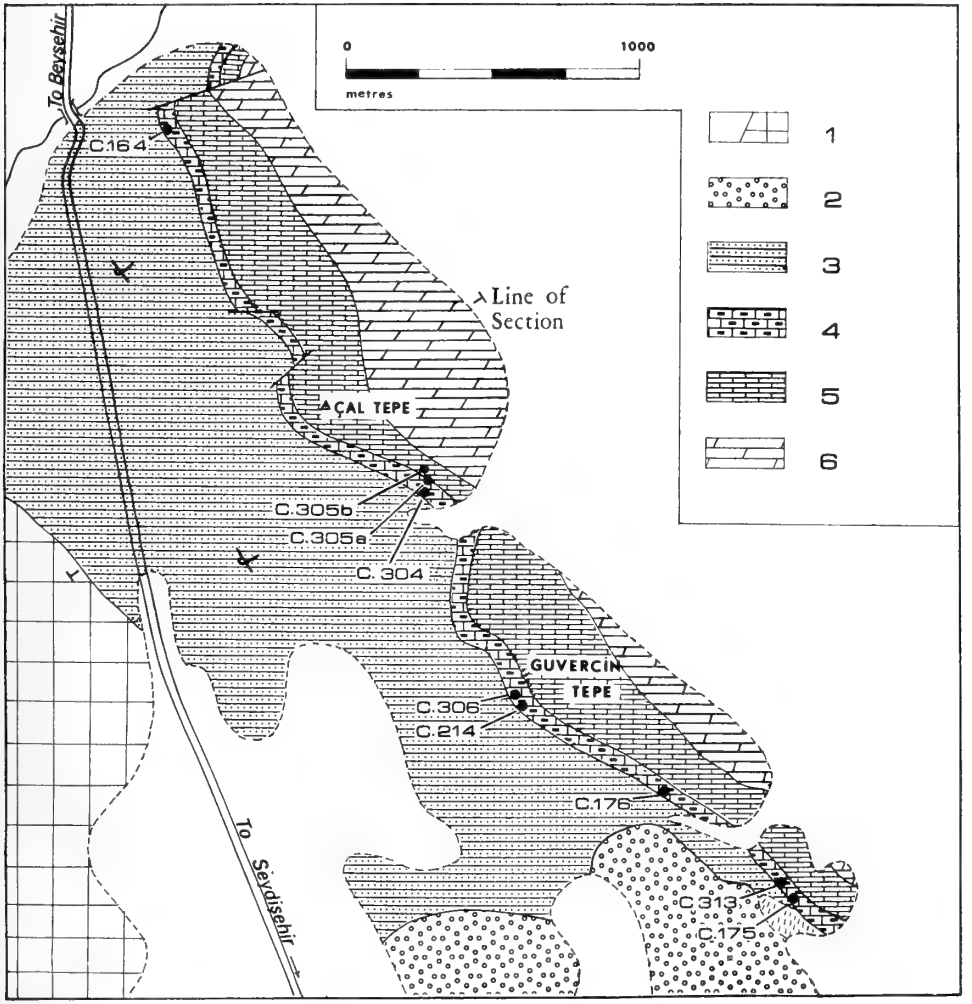

FIG. 3. Fossil localities in the Cambrian rocks of the Çal Tepe district. Geological boundaries by O. Monod. 1 = Recent deposits and Quaternary travertine ; 2 = Upper Neogene conglomerates ; 3 = Seydişehir Shales ; 4–6 = Çal Tepe Formation. 4 = Red nodular limestone ; 5 = Light to dark-grey limestone ; 6 = Dolomite. The broken oblique shading near C.175 denotes superficial talus deposits.

Bed c. comprises well-bedded limestones which are mostly light-grey in colour with occasional patches of pink limestone. Although only about 10 metres thick, this subdivision is of particular importance on account of the fossils it contains.

Locality C.305b., at the southeastern end of Çal Tepe (see Fig. 3), contains the oldest fossils yet known from the area. These comprise fragments of protolenid (?) trilobites together with a large, as yet undetermined form thought to be a paradoxidid, which occur in a pinkish-grey limestone band, a few centimetres thick, near the base of Bed c. Localities C.181 and C.182, from broadly the same horizon but a short distance to the northwest, yielded only unidentifiable trilobite fragments. The material from C.305b. is to receive further study, but if the trilobites are truly protolenids, they would suggest a possible Lower Cambrian age, though an early Middle Cambrian age cannot yet be excluded.

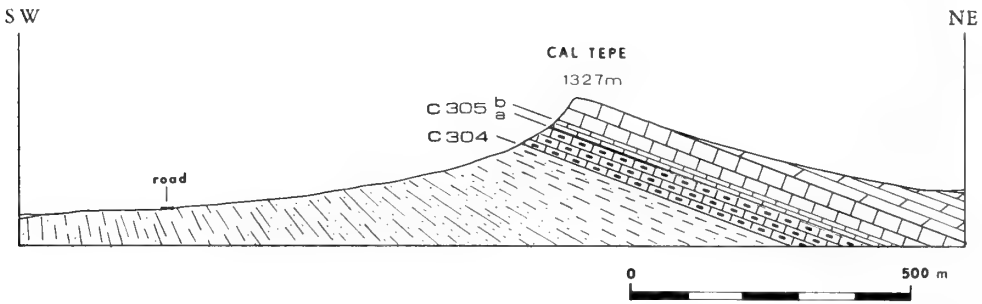

FIG. 4. Cross-section through the Çal Tepe showing the overturned succession of Çal Tepe Limestones and Seydişehir Shales there. For key to Cambrian rocks, see text and Fig. 3.

Also at the southeastern end of Çal Tepe, the highest portion of Bed c. yielded unrecognizable traces of fossils at locality C.183 but nearby, at C.305a., a small faunule of *Corynexochus* sp., *Paradoxides* sp. and fragments of solenopleurids(?) indicated a Middle Cambrian age.

Bed d. is perhaps the most remarkable subdivision of the Cambrian rocks in this area. It consists of thin, irregular beds of red, nodular limestone separated by layers of brownish, argillaceous material. These limestone beds contain only rare fragments of trilobites, but at the top of the subdivision, which may total up to about 40 metres thickness, is the stratum which has yielded the most prolific Cambrian fauna in the district. The latter bed is a grey limestone, in some places with a conchoidal fracture and containing a poor fauna, as at the southeastern end of Çal Tepe ; elsewhere it is rubbly, crumbles readily, and may be highly fossiliferous, as on Guvercin Tepe and the small hill farther southeast. Provisional faunal lists are as follows :—

Locality C.175. *Conocoryphe* sp., *Corynexochus* sp., *Ctenocephalus* sp., *Paradoxides* sp., *Peronopsis* ? sp. *Solenopleuropsis* sp.

Locality C.214. *Conocoryphe* sp., *Corynexochus* ? sp., *Paradoxides* sp.

Locality C.304. *Corynexochus* sp., *Paradoxides* ? sp.

Locality C.313. *Conocoryphe* ? sp., *Corynexochus* ? sp., *Paradoxides* sp., *Peronopsis* sp.

The same horizon crops out on an adjacent hill sited about 1500 metres northwest of Çal Tepe and immediately west of the Beyşehir–Seydişehir road. There, locality C.237 yielded Agraulid (?) gen. et sp., *Corynexochus* sp. and *Paradoxides* sp.

All these trilobites indicate a Middle Cambrian age and are essentially of Tethyan type, similar assemblages of genera having been described from the Western Mediterranean area, Bohemia, the Anglo-Welsh area and eastern Newfoundland. The Çal Tepe Limestone is followed, apparently conformably, by about 50 metres of yellow shales which pass, in turn, into a succession of sandstones and shales. In the latter, one may find occasional lenses of red nodular limestone, of the type forming part of the Çal Tepe Limestone, but all these strata have proved unfossiliferous and they have been included within the Seydişehir Formation. No evidence of Upper Cambrian or Tremadoc faunas has been found in the district.

III. ORDOVICIAN ROCKS: SEYDİŞEHİR FORMATION & SOBOVA FORMATION

The Seydişehir Formation comprises the main detrital series of rocks in the district, and the term is taken to include the Seydişehir Shales *sensu stricto* together with a higher member, the Upper Greywackes. Above the Seydişehir Formation comes a distinct and variable set of beds, consisting of a fossiliferous limestone (the Sobova Limestone) at the base, followed by either red sandstones (at Taraşçı), red shales (at Kızılca) or grey shales (at the Sobova Valley). This group of strata is here termed the Sobova Formation ; it constitutes the uppermost Palaeozoic formation of the region and is overlain disconformably by Mesozoic sediments. As will be demonstrated later, all the fossiliferous strata of the Seydişehir and Sobova Formations belong to the Arenig Series, as far as is now known, but it must be emphasized that no fossils have yet been found in the lower half of the Seydişehir Shales. The Ordovician rocks may be subdivided as follows :—

b. Sobova Formation	Grey shales, passing laterally into red shales and sandstones . .	approx. 20 m.
	Sobova Limestone . . .	0 to 10 m.
a. Seydişehir Formn	Upper Greywackes . . .	approx. 20 m.
	Seydişehir Shales (s.s.) . .	more than 1000 m.

(a) Seydişehir Shales and Upper Greywackes

First named, as Seydişehir-Schiefer, by Blumenthal (1947), the Seydişehir Shales crop out over a considerable area and occupy a tract of country which extends northwestwards from Seydişehir to the village of Kızılca, a distance of some 18 kilometres. A smaller area of outcrop occurs mid-way between Kızılca and Beyşehir, and in this district the small, partially faulted inlier of the Sobova Valley is of considerable stratigraphical importance. Lithologically the Seydişehir Shales consist essentially of a succession of psammitic quartzites alternating with silty, micaceous shales. This monotonous lithology occupies most of the total thickness, which is roughly 1000 metres or more.

Though most of the succession is barren, fossils occur sporadically throughout the upper half of the Seydişehir Shales, and become more frequent towards the top.

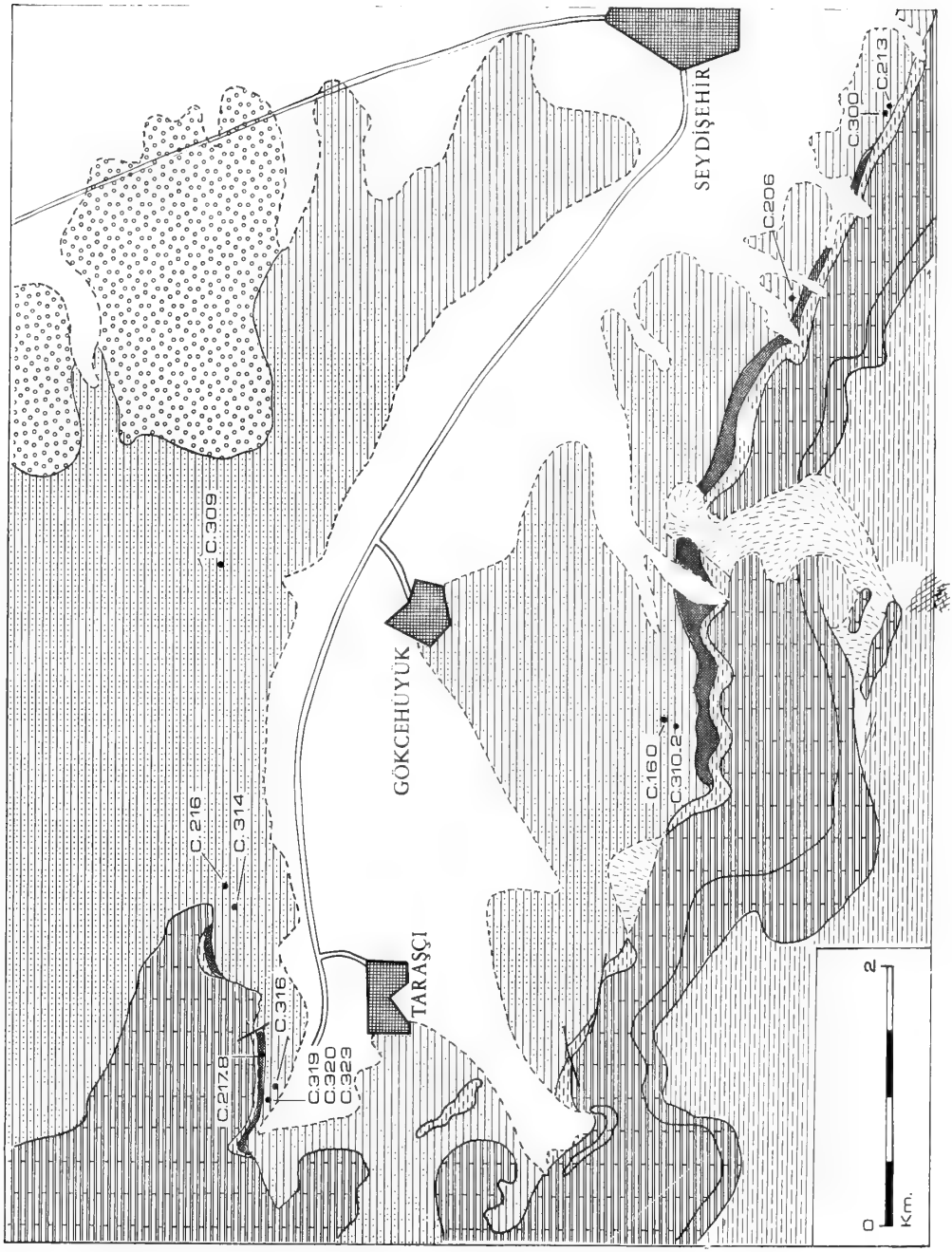

FIG. 5. Fossil localities in the Ordovician rocks near Seydişehir. Key as for Fig. 2 with the following additions :—the Sobova Formation overlying the Seydişehir Formation is indicated by the closely-dotted outcrop ; the shading of discontinuous lines of the overlying strata denotes the lowest Trias (Anisian Stage).

Fossils have now been found at several localities, all of which, for the sake of completeness, are shown on the accompanying maps (see Figs. 5, 6). Few places, however, have yielded identifiable faunas and most of the fossils, though locally abundant comprise poorly-preserved asaphid trilobites, dalmanellid brachiopods, gastropods (*Lesueurilla* sp.) and bivalves (*Redonia* cf. *prisca* Thoral). The shales are generally slickensided and almost invariably barren, and virtually all the fossils were collected from a peculiar, brown-weathering, sandy limestone facies which occurs only in small, thin lenses within the sandstones.

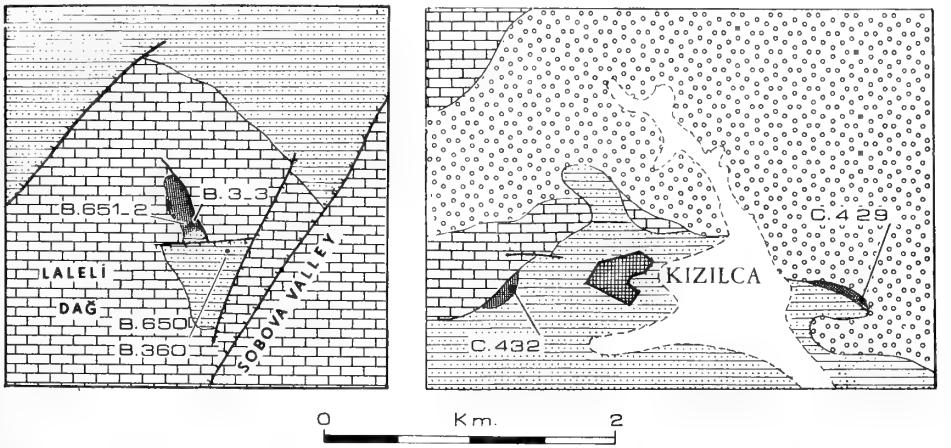

FIG. 6. Fossil localities in the Seydişehir Formation and Sobova Formation in the Sobova Valley and near Kızılca. For key, see Fig. 2, with the addition of the closely-dotted outcrop, which denotes the Sobova Formation, as in Fig. 5. Geological boundaries by O. Monod.

The majority of fossil localities were found west and southwest of Seydişehir, but several occur both at and near the important section to the north of Taraşçı. The latter section (Fig. 7) shows the Seydişehir Shales *sensu stricto* passing conformably upwards into a group of coarser beds, here termed the Upper Greywackes, some 15 metres thick, which are in turn overlain, apparently conformably, by the Sobova Limestone, described later in this paper.

Provisional faunal lists for the Seydişehir Shales (excluding the Sobova Valley outcrop—see later) are as follows :—

Locality C.160. Trilobites—cheirurid ? gen. et sp. indet., *Paramegalaspis* ? sp. Brachiopods—*Cyrtonotella* ? sp., *Panderina* ? sp.
Locality C.216. Trilobites—*Megistaspis* ? sp., *Neseuretus* sp. Brachiopods—*Eodalmanella* sp.
Locality C.310. *Megistaspis* sp., asaphid gen. et sp. undetermined.
Locality C.312. *Megistaspis* sp., asaphid gen. et sp. undetermined.
Locality C.312a. *Megistaspis* ? sp., *Paramegalaspis* ? sp.
Locality C.314. *Megistaspis* ? sp., *Paramegalaspis* ? sp.

In addition to the above shelly fossils, graptolites were collected from localities C.206 and C.310, and we are indebted to Dr. P. Toghill for the following identifications and comments.

" C.206. Numerous fragmentary tetragraptid stipes, all referable to *Tetragraptus* cf. *reclinatus* Elles & Wood, but no complete specimens occur.

C.310. Numerous didymograptid fragments and a few complete examples of *Didymograptus deflexus* Elles & Wood and *D.* cf. *nitidus* Hall.

Although the faunas of these two localities are distinct, they probably represent broadly similar horizons. According to Jackson (1962, p. 308) the acme of reclined tetragraptids was in the Hirundo Zone of the Arenig Series, but in practice they range through both the Extensus and Hirundo Zones. The horizon of C.206 could well be near the boundary between these zones. Similarly the acme of reflexed didymograptids was in the Deflexus Subzone of the Extensus Zone, but they range through both the Extensus and Hirundo Zones. Thus, the horizon of C.310 seems probably to be in the Deflexus or Nitidus Subzones of the Extensus Zone, and is also probably below that of C.206 ".

In the Sobova Valley, 7 kilometres south of Beyşehir, the higher beds of the Seydişehir Shales yielded their most interesting and varied faunas at localities B.360 and B.650 (see Fig. 6). Cephalopods collected by Monod from B.360 were identified by Collins (*in* Monod, 1967, p. 83) as *Bactroceras* sp., *Proterovaginoceras* sp., *Protocycloceras* sp. and a new genus and species, all of which were held to indicate an Arenig age, probably in the upper half of that series. Associated fossils at B.360 include asaphid trilobite fragments, the bivalve *Redonia* cf. *prisca* Thoral, and the gastropod *Lesueurilla* sp.

At locality B.650 the fauna includes the following trilobites :—*Colpocoryphe* sp., *Geragnostus* sp., *Megistaspis* sp., *Paramegalaspis* ? sp. and *Symphysurus* sp.

The terms " calymenid-trinucleid province " (Whittington, 1966) or " Tethyan province " (Dean, 1967) have been employed in previous publications to describe Ordovician faunas of a certain composition in and around the Mediterranean and Western Europe, and it is clear that the faunas of the Seydişehir Shales, with their asaphids, agnostids and calymenaceids, together with *Redonia*, belong in this category. *Symphysurus* is perhaps more indicative of Baltic and Scandinavian faunas, but it has been described from the Montagne Noire, southwestern France, in strata traditionally supposed to be Tremadoc in age, but more probably Lower Arenig. In the present instance the sporadic appearance of *Symphysurus* foreshadows its abundance in the succeeding Sobova Limestone, in which stratum trilobites of Baltic-Scandinavian type predominate.

(b) Sobova Limestone and overlying strata

In the hills about 7 kilometres south of Beyşehir the Sobova Valley contains a small inlier of Seydişehir Shales, roughly triangular in plan with apex directed southwards (see Fig. 6). The southwestern side shows the Ordovician shales overlain unconformably by Jurassic limestones, but the other sides mark the position of faults. The inlier is surrounded by Mesozoic limestones, but a narrow, neck-like outcrop of Ordovician strata extends northwestwards for about 600 metres. In this

outcrop the Seydişehir Shales are succeeded stratigraphically by a group of well-bedded, often massive, jointed, grey and pink detrital limestones, here termed the Sobova Limestone. Most of the beds are unfossiliferous, but many contain unrecognizable crinoid or cystoid ossicles, some contain large concentrations of small brachiopods (*Eodalmanella* sp.), and a few yield what has proved to be the most prolific Ordovician trilobite fauna in the district. With the exception of a single enrolled individual of *Symphysurus*, all the trilobites are represented by isolated fragments, mostly cranidia and pygidia. The strata are available for collecting at only one place on the hill-side, shown on the map as locality B.651 (see Fig. 6). The fauna will be described in detail at a later date, but the provisional list of determinations includes the following :—*Agerina* sp. nov., *Apatokephalus* sp., *Carolinites* sp., *Geragnostus* sp., *Illaenus* sp., *Neseuretus*? sp. indet., *Niobe* sp., *Ampyx* sp. and

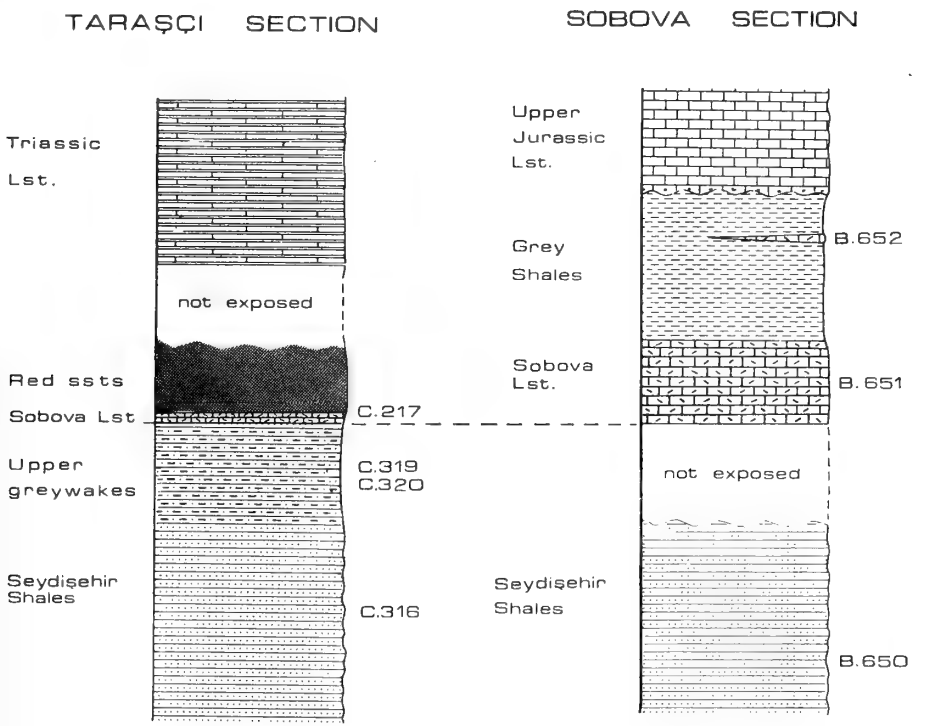

FIG. 7. Sections showing the relationship of the highest Ordovician strata in the Sobova Valley and at Taraşçı. The numbers indicate fossil localities.

Symphysurus sp. The precise dating of this assemblage must await its detailed description, but there is nothing to suggest that it is later than Arenig Series, that is to say not significantly younger than the Seydişehir Shales, so that the junction of the two groups of strata, though not exposed here, is probably conformable, as in the section north of Taraşçı (Fig. 7).

The highest beds of the Sobova Limestone in the Sobova Valley are followed with apparent conformity by a group of grey shales some 20 metres thick. These proved unfossiliferous for the most part, but a thin band of argillaceous limestone at the base of the topmost third yielded a few fragmentary brachiopods and the trilobite *Symphysurus*. The latter genus, present already in the Sobova Limestone and highest Seydişehir Shales, suggests a broadly similar age, i.e. Arenig Series, for the grey shale subdivision which, at this locality, is overlain transgressively by Upper Jurassic limestones.

The section in the Sobova Valley shows the thickest development of the Sobova Limestone, but the thickness diminishes southwards to Taraşçı, where it is only about 2 metres thick at the section northwest of the village (see Fig. 5). There the attenuated development of limestone is succeeded by red sandstones which, from their stratigraphical position, are equivalent to the grey shales of the Sobova Valley. The highest part of the sandstones was not seen at Taraşçı, but the estimated thickness of limestone and sandstone there is about 20 metres, and the rocks are overlain unconformably by Triassic strata, the Taraşçı Limestone (see Monod, 1967, p. 84).

Elsewhere in the Beyşehir–Seydişehir region, fossils have been recovered from the Sobova Limestone at only two places :—locality C.429, about 1·5 kilometres east of the village of Kızılca (see Fig. 6), and locality C.432, just over 0·5 kilometres west of Kızılca. Although the limestone hereabouts is believed to occupy a stratigraphical position at the top of the Seydişehir Shales analogous to that elsewhere, its structural relationships are not clear. Furthermore, the lithology is a white and grey crystalline limestone, often saccharoidal in appearance and generally unlike that at the Sobova Valley, whilst the fauna is quite distinct. The fossils, as at Sobova, consist almost entirely of trilobites, but at C.429 they include the following :—*Cyclopyge* sp., *Euloma* (s.l.) sp., *Symphysurus* ? sp. and an undetermined fragmentary pliomerid.

West of Kızılca, at C.432, the limestone is pink or liver-coloured with grey, crystalline patches, the whole rock being compact, jointed, and cut by numerous thin calcite veins. The limestone there is poorly fossiliferous but contains fragments of *Euloma* (s.l.) sp., *Geragnostus* sp. and *Symphysurus* sp.

Thus, although C.429 and C.432 have broadly similar faunas that are almost certainly of Arenig age, it is still problematical whether they are older or younger than the fauna of B.651. The problem will be discussed again at a later date when the trilobites have been studied in greater detail.

IV. SUMMARY OF CONCLUSIONS

The Cambrian strata of the Beysehir–Seydişehir district are termed the Çal Tepe Formation and total more than 130 metres in thickness. The lower subdivision, the Çal Tepe Dolomite, is unfossiliferous and the base is not exposed. The higher subdivision, the Çal Tepe Limestone, is itself divisible and has yielded trilobites which suggest a possible Lower Cambrian age for the lower beds and a definite Middle Cambrian age for the higher beds, which contain a Tethyan fauna comprising, *inter al.*, *Paradoxides*, *Conocoryphe* and *Ctenocephalus*.

The Çal Tepe Formation is followed by shales of the Seydisehir Formation, which contains Lower Ordovician fossils in its upper half, and at the hill called Çal Tepe

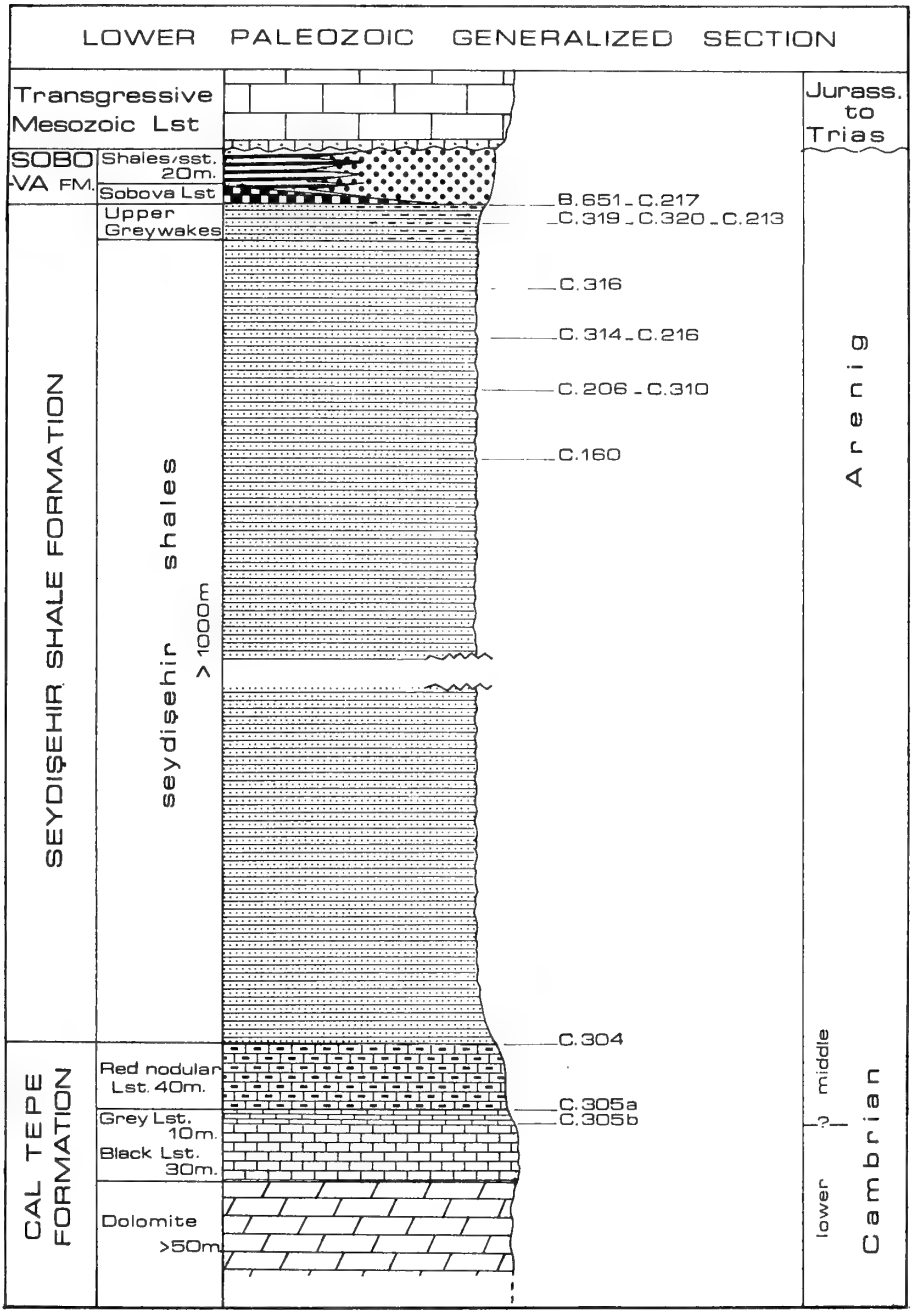

FIG. 8. General stratigraphical succession of the Lower Palaeozoic rocks in the Beyşehir–Seydişehir district.

the succession of the two formations is overturned. The Seydişehir Formation comprises the Seydişehir Shales, a group of silty shales and quartzites more than 1000 metres thick, with a small thickness of Upper Greywackes at the top. The few shelly fossils in the shales are mostly asaphid and calymenid trilobites of Tethyan type, together with graptolites, cephalopods and brachiopods that indicate an Arenig age.

The uppermost Palaeozoic strata, the Sobova Formation, succeed the Seydişehir Formation conformably and comprise the Sobova Limestone (0 to 10 metres thick), followed by a small thickness of shales which passes laterally into red sandstones southwards near Taraşçı. At its type locality, south of Beyşehir, the Sobova Limestone contains a trilobite fauna of predominantly Baltic-Scandinavian affinities that includes *Agerina, Carolinites, Illaenus, Niobe* and *Symphysurus*. A few Tethyan genera occur also, and the fauna is of Arenig age. Over the whole region the substratum of older Palaeozoic rocks is overlain unconformably by Mesozoic limestones.

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